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The genus *Andrena* Fabricius, 1775 in the Iberian Peninsula (Hymenoptera, Andrenidae)

Thomas J. Wood[1]

1 *University of Mons, Research Institute for Biosciences, Laboratory of Zoology, Place du Parc 20, 7000, Mons, Belgium*

Corresponding author: Thomas J. Wood (thomasjames.wood@umons.ac.be)

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Abstract

The Iberian Peninsula is a global hotspot for bee diversity due to its large number of different habitats, particularly Mediterranean scrubland, mountains, and hot and cold steppe. In line with its status as a hotspot of bee diversity, the peninsula hosts a very large *Andrena* fauna, which despite progress in recent years remains incompletely studied, particularly with reference to genetic investigation. Here the Iberian *Andrena* fauna is comprehensively revised, resulting in a total of 228 recorded species. Numerous taxonomic changes are necessary following inspection of museum specimens, type material, and genetic investigation. The following subgenera are described: *Pruinosandrena* **subgen. nov.**, containing six taxa previously placed in the subgenus *Campylogaster* Dours, 1873, and *Blandandrena* **subgen. nov.**, *Bryandrena* **subgen. nov.**, *Limbandrena* **subgen. nov.**, and *Ovandrena* **subgen. nov.**, containing one, one, one, and four taxa previously placed in the subgenus *Poliandrena* Warncke, 1968. *Andrena* (*Limbandrena*) *toelgiana* Friese, 1921 **syn. nov.** is synonymised with *A.* (*Limbandrena*) *limbata* Eversmann, 1852. The current lectotype of *A.* (*Micrandrena*) *obsoleta* Pérez, 1895 was incorrectly designated by Warncke; the taxon differs from *A. obsoleta* sensu Warncke, belonging instead to a taxon within the *A. mariana* Warncke, 1968 complex. A new lectotype is designated for *A. obsoleta* **sp. resurr.** from Algeria, and *A. mariana solda* Warncke, 1974 **syn. nov.** is synonymised with it; *A.* (*Micrandrena*) *alma* Warncke, 1975 **stat. nov.**, *A.* (*Micrandrena*) *mica* Warncke, 1974 **stat. nov.**, and *A.* (*Micrandrena*) *tenostra* Warncke, 1975 **stat. nov.** are raised to species status. *Andrena* (*Truncandrena*) *abunda* Warncke, 1974 **stat. nov.**, *A.* (*Micrandrena*) *lecana* Warncke, 1975 **stat. nov.**, *A.* (*Pruinosandrena*) *parata* Warncke, 1967 **stat. nov.**, *A.* (*Micrandrena*) *pauxilla* Stöckhert, 1935 **sp. resurr.**, *A.* (*Pruinosandrena*) *succinea* Dours, 1872 **sp. resurr.**, and *A.* (*Notandrena*) *varuga* Warncke, 1975 **stat. nov.** are also returned or elevated to species status. A lectotype is designated for *A.* (*Euandrena*) *lavandulae* Pérez, 1902 **sp. resurr.** which is returned to species status, and *A.* (*Euandrena*) *impressa*

Warncke, 1967 **syn. nov.** is synonymised with it. *Andrena* (*Truncandrena*) *nigropilosa* Warncke, 1967 **stat. nov.** is elevated to species status, and *A.* (*Truncandrena*) *truncatilabris espanola* Warncke, 1967 **syn. nov.** is synonymised with it as a junior subjective synonym. A lectotype is designated for *A.* (*Melandrena*) *vachali* Pérez, 1895; *A.* (*Melandrena*) *creberrima* Pérez, 1895 **syn. nov.** and *A.* (*Melandrena*) *vachali* **syn. nov.** are synonymised with *A.* (*Melandrena*) *discors* Erichson, 1841, and *Andrena* (*Melandrena*) *hispania* Warncke, 1967 **syn. nov.** is synonymised with *A.* (*Melandrena*) *morio* Brullé, 1832. *Andrena* (*Pruinosandrena*) *mayeti* Pérez, 1895 **syn. nov.** is newly synonymised with *A.* (*Pruinosandrena*) *caroli* Pérez, 1895 and *A.* (incertae sedis) *setosa* Pérez, 1903 **syn. nov.** is newly synonymised with *A.* (incertae sedis) *ranunculorum* Morawitz, 1877. *Andrena* (*Simandrena*) *cilissaeformis* Pérez, 1895 **sp. resurr.** is returned to species status, and is the correct name for *A.* (*Simandrena*) *breviscopa* auctorum. *Andrena* (incertae sedis) *breviscopa* Pérez, 1895 is returned to synonymy with *A.* (incertae sedis) *numida* Lepeletier, 1841, and *A.* (incertae sedis) *inconspicua* Morawitz, 1871 is newly synonymised **syn. nov.** with *A. numida*. *Andrena* (*Euandrena*) *isolata* **sp. nov.** and *A.* (*Micrandrena*) *ortizi* **sp. nov.** are described from the Sierra Nevada (Granada), *A.* (*Truncandrena*) *ghisbaini* **sp. nov.** is described from Málaga province, and *A.* (*Avandrena*) *juliae* **sp. nov.** is described from Cádiz province. The males of *A.* (*Micrandrena*) *alma* and *A.* (*?Euandrena*) *ramosa* Wood, 2022 are described. Additional lectotypes are designated for *A.* (*Plastandrena*) *asperrima* Pérez, 1895, *A.* (*Plastandrena*) *atricapilla* Pérez, 1895, *A.* (*Aenandrena*) *hystrix* Schmiedeknecht, 1883, *A.* (*Pruinosandrena*) *lanuginosa* Spinola, 1843, *A.* (*Notandrena*) *ranunculi* Schmiedeknecht, 1883, and *A.* (*Euandrena*) *symphyti* Schmiedeknecht, 1883. Neotypes are designated for *A.* (*Chlorandrena*) *boyerella* Dours, 1872, *A.* (*Notandrena*) *griseobalteata* Dours, 1872, *A.* (*Taeniandrena*) *poupillieri* Dours, 1872, *A.* (*Pruinosandrena*) *succinea* Dours, 1872, and *A.* (incertae sedis) *numida* Lepeletier, 1841. Type photographs and diagnostic characters are presented in each case, as well as new dietary information for understudied species. Finally, an identification key is presented in order to facilitate future research on this hyper-diverse genus in one of their global diversity hotspots, and current and future research perspectives for Iberian *Andrena* are discussed.

Keywords
Cryptic species, DNA barcoding, Iberian endemic species, solitary bees, taxonomy

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Introduction

The Iberian Peninsula is one of the best places to find and study wild bees globally, with more than 1,000 species present due to its dry and warm climate, abundance of open seasonal habitats, status as a glacial refugium, and rich diversity of flowering plants (Lhomme et al. 2020; Ortiz-Sánchez 2020; Orr et al. 2021). Within this large fauna, the most speciose element consists of bees from the genus *Andrena* which are abundant throughout the peninsula and which are a ubiquitous component of the spring pollinator community. This pattern is typical for the Holarctic, as *Andrena* are the second largest genus of bees globally with around 1,650 species following recent revisions (Ascher and Pickering 2020; Pisanty et al. 2022a; Wood and Monfared 2022) and are almost always the most speciose genus in regional faunas across this region. Considering that bees emerged in the early to mid-Cretaceous period 110–140 million years ago (Danforth et al. 2013; Branstetter et al. 2017; Murray et al. 2018), as a major bee genus *Andrena* is relatively young, arising around 25 million years ago (Pisanty et al. 2022b). Given the size of the genus, *Andrena* has speciated extremely quickly (Bossert et al. 2022), leading to enormous species richness and often extreme taxonomic difficulty in delineating and recognising species. Given the abundance and ubiquity of this genus in the Iberian fauna, it is desirable to have suitable taxonomic resources to enable study of this rich fauna. However, nothing resembling an accessible revision is currently available.

Despite the great number of species present in Iberia, very few authors have worked on this fauna in any detail, certainly compared to that of north-western Africa (e.g. Erichson 1841; Lepeletier 1841; Dours 1872, 1873; Pérez 1895, 1902, 1903; Morice 1899; Schmiedeknecht 1900; Saunders 1908; Benoist 1961). Somewhat incredibly, before 2020, only six papers were published that described currently valid *Andrena* species with a *locus typicus* in Iberia: Erichson (1835, three species), Dours (1873, one species), Pérez (1895, six species), Pérez (1902, one species), Warncke (1967, 10 species), and Warncke (1975a, 15 species), although some other works described what are now synonymous names (e.g. Spinola 1843; Pérez 1903; Friese 1922). The fauna was therefore quite unstudied before the revisionary work of Warncke (1967, 1975a, 1976), and following these publications almost no additional taxonomic work was carried out on the Iberian fauna until very recently. This attention has come in the form of revisionary taxonomic work and faunal work that has provided new distributional records, demonstrated the presence of doubtful species in Iberia, and recorded new species for the Iberian *Andrena* fauna (Baldock et al. 2018; Álvarez Fidalgo et al. 2020, 2021a, 2021b, 2022a, 2022b; Wood et al. 2020a, 2021, 2022; Álvarez Fidalgo and Aguado Martín 2022; Wood 2022; Wood and Ortiz-Sánchez 2022).

As a result of these collective efforts, our understanding of Iberian *Andrena* is as great as it has ever been. However, commencing ecological or taxonomic work on this fauna remains highly challenging due to the lack of accessible identification resources. Valuable information is available in original descriptions, group revisions (e.g. Schwenninger 2015), and treatments on other regional faunas (e.g. Schmid-Egger and Scheuchl 1997; Amiet et al. 2010), as well as in the global revisionary catalogue of Gusenleitner and Schwarz (2002). However, digging through this mountain of infor-

mation is time consuming and sometimes dispiriting and confusing, in part due to persistent problems with species concepts and taxonomic nomenclature. It is therefore the objective of this present paper to resolve most of the outstanding taxonomic problems with the Iberian *Andrena* fauna and to present a new synthesis of this information in the form of a comprehensive identification key. Due to the strong faunal links between North Africa and Iberia, it is necessary to revise parts of the North African *Andrena* fauna in parallel; a subsequent paper dealing with taxonomic revisions exclusive to the North African *Andrena* fauna will follow shortly. Therefore, several taxonomic changes will be made here that affect the North African fauna, although this is not the principal objective of the current work. Finally, novel ecological data are provided concerning the pollen foraging niche of unstudied Iberian or West Mediterranean *Andrena* species.

Methodology

Species concepts

It is important to briefly discuss species concepts in the context of this work. Because *Andrena* taxonomy in the West Palaearctic region was dominated by Klaus Warncke in the second half of the 20th Century, it is his classification system that has largely been followed by subsequent workers (e.g. Gusenleitner and Schwarz 2002). Warncke recognised species solely based on their morphology, and used subspecies to delineate geographical variation. Subsequent workers have treated many of these subspecies as valid species based on morphological, genetic, and ecological data (e.g. Gusenleitner and Schwarz 2002; Schmid-Egger 2005; Schwenninger 2015; Praz et al. 2019; Kratochwil 2021; Wood et al. 2021; McLaughlin et al. 2022; Pisanty et al. 2022a).

To date, there has not been a deep discussion of species concepts in *Andrena* compared to better studied bee groups such as bumble bees (*Bombus*, e.g. Williams et al. 2020; Rasmont et al. 2021). Use of a purely biological species concept in *Andrena* is premature in almost all cases as we have extremely limited understanding of their mating systems and pre- and post-zygotic reproductive barriers, with this only being estimated *post hoc* by quantifying realised gene flow (e.g. McLaughlin et al. 2022). Given that the study of *Andrena* taxonomy using genetics is still in its infancy, it is best to consider *Andrena* species to be evolutionarily independent lineages (de Queiroz 2007), and that through the application of integrative taxonomy (including genetic, morphological, and ecological data), one can arrive at a robust species concept (Schlick-Steiner et al. 2010).

As such, the present work builds on the morphological species concepts developed by previous workers and integrates genetic and ecological lines of evidence in order to ensure evidence-based species delineation. In this context, subspecies are used pragmatically, following the position of Mayr (1963, see Rasmont et al. 2021) and drawing from the taxonomic heritage of Warncke's West Palaearctic revisions. Where sufficient data are available, these subspecies are validated as species in their own right or synonymised. Where such data are not available or the results are ambiguous, subspecies are retained in order to indicate future avenues of taxonomic study.

Genetic sampling and analysis

Andrena specimens were sampled in Iberia and Morocco, predominantly during May–July 2021 in Spain and March–July 2022 in Morocco, but also using specimens collected in previous years. For genetic barcoding, a single midleg was removed from pinned specimens and sent to the Canadian Center for DNA barcoding (CCDB) in Guelph, Canada, for DNA extraction and sequencing (Ivanova et al. 2006). Specimens were sequenced following standardised high-throughput protocols. Both Lep1 and BeeCox1F1 primers were used (Hebert et al. 2004; Bleidorn and Henze 2021) to target the COI-5 region. All sequences are published on the Barcode of Life Database (BOLD) website under the public dataset “DS-ANDWMED”.

Phylogenetic trees were supplemented with additional published sequences (e.g. Schmidt et al. 2015) that were downloaded from Genbank and the Barcode of Life Data System. Trees were also significantly enriched with sequences produced by the Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO, Portugal) as part of a collaboration to barcode the Portuguese bee fauna that will be published in the near future, and sequences will be available on BOLD. Sequences beginning with the code ‘IBIHM’ were generated by CIBIO. Sequences were aligned using MAFFT (Katoh and Standley 2013). Aligned sequences were analysed in Seaview (Gouy et al. 2010) using a maximum likelihood analysis which was run with 1000 bootstraps. Intra- and interspecific distances were calculated using MEGA-X (Kumar et al. 2018). Outgroups were chosen based on the subgeneric analysis of Pisanty et al. (2022b) in order to ensure that the selected outgroup species is part of a subgenus or species group more basal to those selected for focused study.

Taxonomic decisions were informed by analysis of the COI gene. However, decisions were not taken exclusively on the basis of these analyses, as there are a number of inherent limitations when using this fragment to inform taxonomy. The COI fragment itself only represents a single locus of mitochondrial DNA which is inherited matrilineally, can introgress across species boundaries, can transfer to the nuclear genome, cannot detect hybridisation, and can produce topologies that do not represent species trees (e.g. Toews and Brelsford 2012). Species delineation based solely on differences in mitochondrial DNA is therefore discouraged, with integrative taxonomic preferred (Padial et al. 2010; Gallego-García et al. 2023). More broadly, more powerful genetic techniques are now available such as Ultra Conserved Elements that allow the generation of sequences from thousands of loci. These have been applied to bee taxonomy at the species-level, and whilst they often produce results concordant with COI analysis (e.g. de Oliveira Andrade et al. 2022; McLaughlin et al. 2022), they can also clearly resolve problems for which COI analysis produces ambiguous or inconclusive results (e.g. Gueuning et al. 2020). However, to date, UCEs have predominantly been employed to resolve specific questions, and not to sample across a fauna in order to have the broadest possible taxonomic coverage, as was the objective in this study. Given these limitations, combined with the conceptual points discussed above, analysis of the COI fragment is used as an additional line of evidence to support taxonomic decision making, and is never used as the sole metric.

More broadly, COI analysis is most useful when dealing with species-specific alpha taxonomic decisions. Due to the rate at which this fragment accumulates mutations, whilst closely related species are grouped together, more distantly related species often show no clear structuring and the true evolutionary relationships are not captured. For this, more conserved genes must be sampled, such as by using UCEs. In this work, several new *Andrena* subgenera are described and illustrative phylogenetic trees are presented based on analysis of the COI fragment; the description of these subgenera is based on the work of Pisanty et al. (2022b) who identified undescribed clades of *Andrena*. These clades were not discovered here through analysis of the COI fragment, and these illustrative phylogenetic trees should not be considered strong support for their existence.

Finally, there are several cases presented here where morphological and genetic data produce ambiguous results concerning the status of certain taxa. Several of these taxa are widespread, and are usually described from outside of the Iberian Peninsula (e.g. see problems with paraphyly of *A. hedikae* Jäger, 1934). In these cases, no taxonomic action is taken, as it is preferable to have topotypic genetic samples and to consider these taxa across their entire nominal range. Where multiple valid species are potentially present, these species are referred to using the phrase 'aggregate' to reflect this situation. In contrast, when species are described from Iberia or have ranges that are restricted to the peninsula or to the West Mediterranean region, taxonomic decisions can be and are made with a greater degree of confidence which reflects the stronger and more complete evidence base available here.

Checklist and identification

For updating the Iberian *Andrena* species total, the checklist of Ortiz-Sánchez (2020) for mainland Spain and Portugal is used as a baseline. As this list is mostly correct, it is not considered necessary to produce a full annotated list for the Iberia *Andrena* fauna here; instead, a detailed justification will be given for the changes which have been made since 2020 or which are newly made here. A full checklist is provided in Suppl. material 1.

Identification key and geographic scope

For the identification keys, the female key is partly based on an unpublished key to Iberian *Andrena* written by Klaus Warncke (in German) that was kindly shared with me by Erwin Scheuchl (Ergolding, Germany). This key contained around 170 species, so considerable modifications were needed to account for the substantially larger faunal total recorded here, as well as accounting for newly described species and other taxonomic changes. The male key is novel, but both the female and male keys have been strongly inspired by the keys of Schmid-Egger and Scheuchl (1997) and Amiet et al. (2010). Additional characters have also been integrated from published works such as Schönitzer et al. (1995), Schwenninger (2009, 2013, 2015), and Praz

et al. (2019, 2022). It is not always easy to remember the precise source of specific characters used here that have been accumulated and integrated over several years of study, as many are scattered throughout the literature in original descriptions, some derive from my own observations, and many are taken from the important diagnostic characters that are embedded throughout Gusenleitner and Schwarz (2002), but which can be somewhat obscure and hidden in individual species accounts. It is my hope that this key can bring this information together as a novel synthesis, becoming a more easily digestible resource.

The geographic scope of the key is limited to the Iberian Peninsula. It cannot be used in North Africa due to the many different or endemic faunal elements found there; for example, it only covers 114 of the 201 (56.7%) *Andrena* species known from Morocco (Wood in prep.). In a European context, the key can be used in the Balearic Islands, though only a fraction of the species covered in this work occur there. It can be generally used in southern France up to (but not including) the Maritime Alps, but some taxa are missing, such as endemic species (e.g. *Andrena* (*Taeniandrena*) *vocifera* Warncke, 1975) or widespread European species that do not cross the Pyrenees into Iberia (e.g. *Andrena* (*Micrandrena*) *pusilla* Pérez, 1903). However, the existing keys of Schmid-Egger and Scheuchl (1997) and Amiet et al. (2010) can be used in conjunction with this Iberian key to cover the vast majority of the *Andrena* fauna of southern France. The Iberian key should not be used in an Italian context as the Italian fauna is already sufficiently distinct to render the key of limited use, either in northern Italy due to the presence of eastern faunal elements (e.g. *Andrena* (*Aenandrena*) *bisulcata* Morawitz, 1877) or in Sicily due to the large number of non-Iberian North African elements present there, and also because many Iberian taxa are absent from the Italian fauna which has a much lower degree of endemism. Finally, this key should not be used in Corsica or Sardinia, as their island faunas require dedicated study due to the presence of endemic and North African species, as well as local forms or subspecies.

Distribution maps

No distribution maps are presented as part of this work, as they are for other revisions such as that of Ortiz-Sánchez and Pauly (2017). This is because whilst the material that I have examined, validated, and digitised is sufficient to allow a more or less complete taxonomic understanding of the Iberian fauna, it is not sufficiently geographically comprehensive, and hence distribution maps would be incomplete at the scale of the peninsula. Moreover, the distribution maps of Warncke presented by Gusenleitner and Schwarz (2002) are sufficiently correct to be informative to students of the Iberian fauna, with the assumption that the updated taxonomy presented here and by other workers after 1993 is integrated. Important distributional information is given in the text where relevant, and also in the identification key, as many taxa (particularly Euro-Siberian taxa) are geographically limited and the place of capture can strongly inform their identification (e.g. species restricted in an Iberian context to the Pyrenees, to central or southern Spain, etc).

Dietary niches of Iberian *Andrena* species

Pollen was removed from female *Andrena* specimens in order to quantify the pollen foraging niche of understudied species. Specimens were selected from Iberia and other Mediterranean countries when the species' range extends beyond the peninsula. Pollen was removed, processed, and identified following the methodology of Wood and Roberts (2018). Dietary classification (polylecty, mesolecty, oligolecty, narrow oligolecty) follows Müller and Kuhlmann (2008).

Morphological terminology

Morphological terminology follows Michener (2007). Specimens were measured from the centre of the clypeus at the front of the head to the apical tip of the metasoma to the nearest 0.5 mm. Photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 5X infinity corrected objective lens. Photographs were stacked using Helicon Focus B (HeliconSoft, Ukraine) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Post-processing of some images was made in Photoshop Elements (Adobe Systems, USA) in order to improve lighting to highlight specific characters.

The following abbreviations are used in the species descriptions: **A** = antennal segments, **S** = metasomal sterna, and **T** = metasomal terga. Subgeneric concepts follow Pisanty et al. (2022b) with the necessary modifications detailed below. In diagnoses, the defining characters of a species are given, with those of the indicated comparison species given in parentheses.

Collections studied

AMC Personal collection of Andreas Müller, Wädenswil, Switzerland;
CMHC Carlos M. Herrera collection, Estación Biológica de Doñana, Seville, Spain;
FJOS Personal collection of Francisco Javier Ortiz-Sánchez, El Ejido, Spain;
FLOW FLOWer lab collection, University of Coimbra, Coimbra, Portugal;
EBDC EBD-CSIC collection, Estación Biológica de Doñana, Seville, Spain;
MNHN Muséum national d'Histoire naturelle, Paris, France;
MRSN Museo Regionale di Scienze Naturali di Torino, Turin, Italy;
MSC Personal collection of Maximillian Schwarz, Ansfelden, Austria;
MZUR Zoological Museum of Sapienza University of Rome, Rome, Italy;
NHMUK Natural History Museum, London, United Kingdom;
OÖLM Oberösterreiches Landesmusum, Linz, Austria;
RMNH Naturalis Biodiversity Center, Leiden, the Netherlands;
SMFD Naturmuseum Senckenberg, Frankfurt am Main, Germany;
TJWC Personal collection of Thomas J. Wood, Mons, Belgium;
UMONS Laboratory of Zoology collection, University of Mons, Mons, Belgium;
ZISP Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia;
ZMHB Museum für Naturkunde, Berlin, Germany.

Results

Genetic results and taxonomic changes

Genetic study of Iberian *Andrena* resulted in a number of important necessary changes to species concepts, as well as further supporting recent decisions. These results are presented here by subgenus; not all Iberian *Andrena* subgenera are treated here, as no taxonomic problems were detected for the majority of species.

Subgenus *Aciandrena* Warncke, 1968

In Iberia, this is a species-poor subgenus, consisting solely of *A. fulica* Warncke, 1974 and *A. vacella* Warncke, 1975. Warncke described *A. astrella* Warncke, 1975 from Iberia, and used it in combination with *A. fulica* as a subspecies. The two taxa were synonymised by Wood et al. (2020b) as one of the distinguishing characters was that North African populations had males with the clypeus entirely black, and Iberian populations had males with the clypeus yellow-marked, but males with both colour forms can be found in both geographical regions. There are no clear structural differences in the tergal punctation or the structure of the male genital capsule. Genetically (Fig. 1), Iberian and Moroccan populations differ by an average genetic distance of 1.61% (range 1.31–2.09%). Although Iberian material (including specimens WPATW318-21 and WPATW354-21 which are black-faced males from the Sierra Nevada) forms a clade with bootstrap support of 100, the overall low genetic distance is not considered to be sufficient to justify species status. The synonymy of Wood et al. (2020b) is therefore maintained. The broad *A. fulica* clade as a whole is well-defined with bootstrap support of 98.

Subgenus *Aenandrena* Warncke, 1968

This subgenus was found to be paraphyletic by Pisanty et al. (2022b), and the same result is found here with a COI-based analysis (Fig. 1). *Andrena hystrix* Schmiedeknecht, 1883 falls away from *A. aeneiventris* Morawitz, 1872 and *A. hedikae* Jäger, 1934. For convenience, these taxa are retained in the same subgenus, but future work will be needed to resolve this issue and probably to describe a new subgenus for the species around *A. hystrix* (currently three Palaearctic species from Morocco to Central Asia). Type material for *A. hystrix* was recently rediscovered, and a lectotype for this species is designated below.

In the true *Aenandrena*, four species are currently recognised, of which two are widely distributed, *A.* (*Aenandrena*) *aeneiventris* Morawitz, 1872 that was described from Italy and *A.* (*Aenandrena*) *hedikae* Jäger, 1934 that was described from the western Balkans. Both of the widespread species are nominally distributed from Iberia and Morocco to Central Asia in dry and warm parts of the Palaearctic (Gusenleitner and Schwarz 2002). Barcode analysis (Fig. 1) showed that *A. aeneiventris* specimens from Austria, Hungary, Israel, and Portugal formed a clade with bootstrap support of 99,

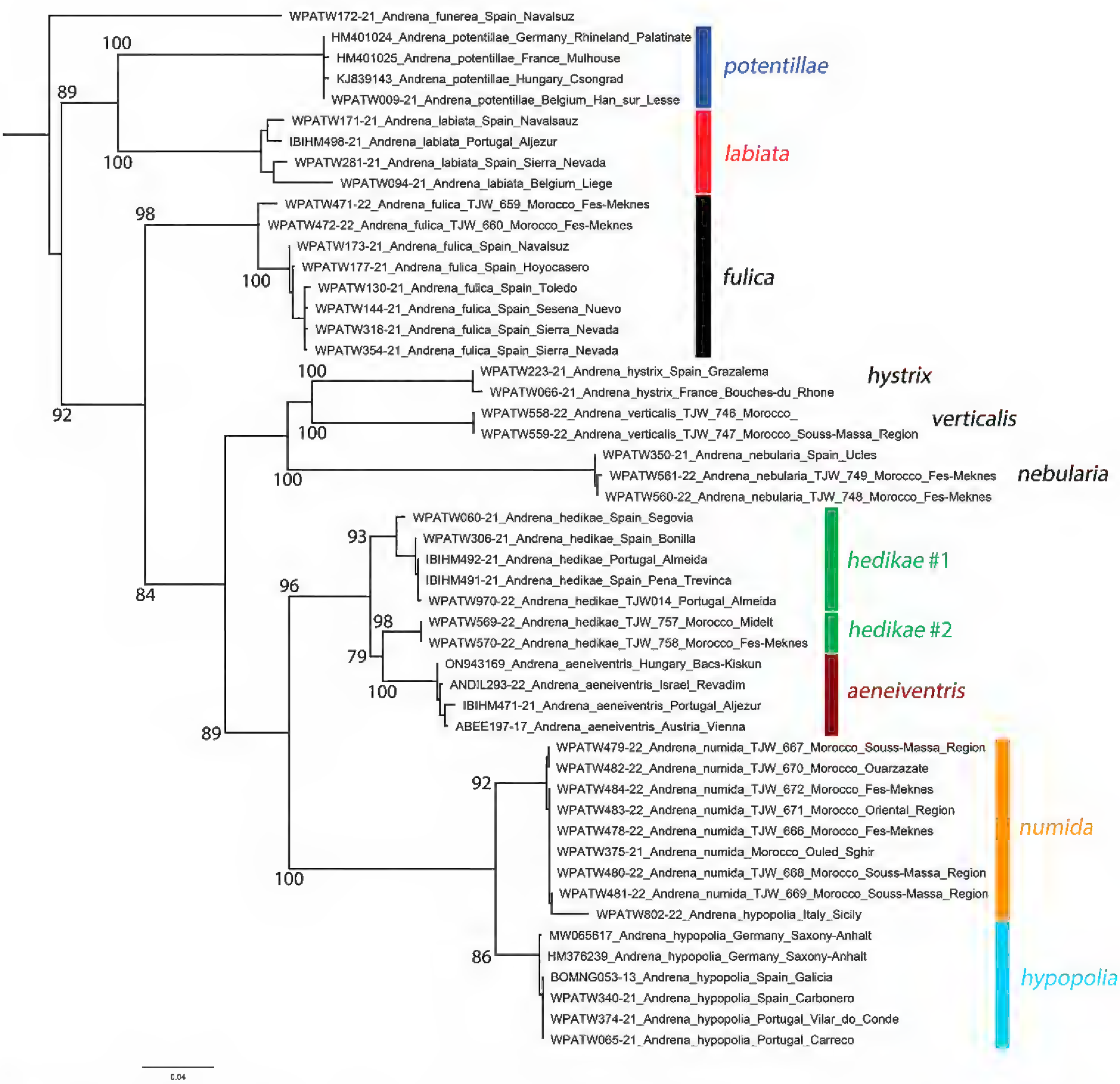

Figure 1. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Aciandrena* Warncke, 1968, *Aenandrena* Warncke, 1968 sensu lato, *Graecandrena* Warncke, 1968, *Poecilandrena* Hedicke, 1933, and the *numida*-group based on the mitochondrial COI gene. *Andrena* (incertae sedis) *relata* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

and with low average intraspecific genetic distance of 0.78% (range 0.30–1.06%). In contrast, *A. hedikae* formed two clades. Five specimens from Portugal and Spain formed a clade with bootstrap support of 93 with low differentiation of 0.82% (range 0.16–2.01%). Two specimens from northern Morocco had identical sequences and formed a clade with bootstrap support of 98. These two clades were separated by an average genetic distance of 4.55% (range 4.34–4.72%), and both were well-separated from *A. aeneiventris*, by an average genetic distance of 5.86% (range 4.98–6.67%) for Iberian specimens and 5.20% (range 4.86–5.75%) for Moroccan specimens. These genetic distances are substantial, but no taxonomic action is taken here, as sequences from south-eastern Europe are needed to i) further understand barcode variation in

A. hedikae and ii) identify which of these two clades matches populations from the *locus typicus*. Moreover, there are no apparent morphological differences between Iberian and Moroccan '*hedikae*'. Further study is required.

Subgenus *Chlorandrena* Pérez, 1890

This subgenus is clearly supported genetically (Pisanty et al. 2022b) and morphologically by the presence of a row of teeth on the posterior face of the female femur combined with strong 'crater punctures' on the terga. Barcodes generally supported all species concepts (Fig. 2), but there are some issues that must be discussed.

Andrena (*Chlorandrena*) *livens* Pérez, 1895 was described from north-eastern Spain. Warncke described *A. livens algeria* Warncke, 1967 from Tunisia on the basis of slight

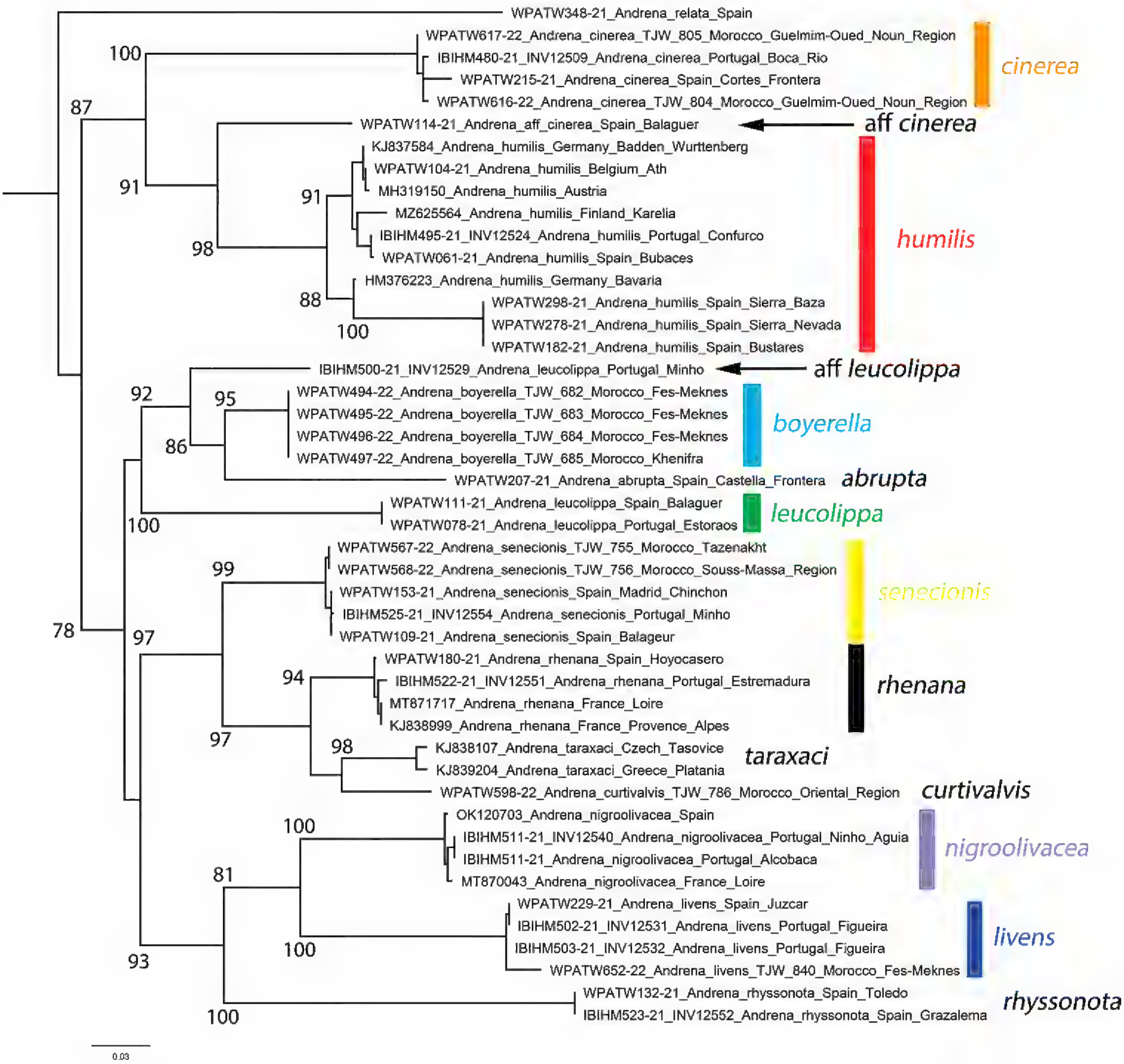

Figure 2. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Chlorandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (*Nobandrena*) *funerea* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

differences in the genital capsule and sternum eight. He also described *A. livens gruenwaldti* Warncke, 1967 from Sicily. Based on the sequences here, a Moroccan specimen conforming to *A. livens algeria* shows relatively low differentiation from Portuguese and Spanish specimens, being separated by an average genetic distance of 2.37% (range 2.16–2.47%). Additional samples are required to investigate the status of these subspecies, and also to sample *A.* (*Chlorandrena*) *agnata* Warncke, 1967 which is a poorly understood species in an Iberian context; I have seen no Iberian specimens, and it is included on the list on the basis of the single female paratype from Madrid, collected 6.vi.1946 by Dusmet (Warncke 1967). *Andrena agnata* is much closer morphologically to *A. livens* than the nearest neighbour in the current tree, *A.* (*Chlorandrena*) *nigroolivacea* Dours, 1873; no taxonomic action is taken until such sequences are available, and a broad *A. livens* concept is maintained for now.

The status of *A.* (*Chlorandrena*) *boyerella* Dours, 1872 and *A.* (*Chlorandrena*) *leucolippa* Pérez, 1895 and the relationship of these taxa to each other has been confused. Warncke (1967) used a subspecies concept, with *A. boyerella* s. str. present in North Africa and *A. boyerella leucolippa* present in Iberia and France, *A. leucolippa* being described from south-western France, *locus typicus* Riscle (Fig. 3). It is important to note that Pérez writes in his catalogue under entry 442 that he had males from Algeria; in any case, the designation of the lectotype by Warncke (1967) from France fixes this name unambiguously on European populations. North African and Iberian specimens differ, with *A. leucolippa* presenting denser tergal punctation, in the male sex the yellow colouration of the clypes extends onto the mandibles and the lower paraocular areas (only the clypeus is yellow-marked in *A. boyerella*), and there are slight differences in the genital capsule. Gusenleitner and Schwarz (2002) listed *A. leucolippa* as a distinct species.

However, this classification is not immediately stable due to the fact that the type series of *A. boyerella* is lost, as is the case for all of Dours' types. Dours (1872) described *A. boyerella*, and there is no doubt over the morphological identity of this taxon based on the clear description. However, Dours gives a distribution of southern France and Algeria. It is therefore the case that, if there are two different species, then Dours' type series was polytypic. Warncke (1967) and Gusenleitner and Schwarz (2002) give the *locus typicus* of *A. boyerella* as Algeria, but since there is no holotype or designated lectotype, the *locus typicus* is undefined. Genetically, sequences from four North African specimens from the Middle Atlas in Morocco were identical and formed a clade (Fig. 2) that was strongly separated from two sequences from Estorãos near Fafe in northern Portugal [WPATW078-21] and Balaguer in Catalonia in north-eastern Spain [WPATW111-21] by an average genetic distance of 13.27% (range 13.27–13.27%). The two clades are not sisters, being separated by *A.* (*Chlorandrena*) *abrupta* Warncke, 1967. The matter would appear to be clear, that two taxa are present. However, a specimen from Vieira do Minho in northern Portugal [IBIHM500-21] diverged from both these lineages, being separated from the Moroccan sequences by 8.95% and the two other Iberian sequences by 14.51%. This site is only 16 km from the Estorãos site. Morphologically, there are no obvious differences; all three Iberian specimens are males. Because *A. leucolippa* was described from south-western France, the sequence from north-eastern Spain is here

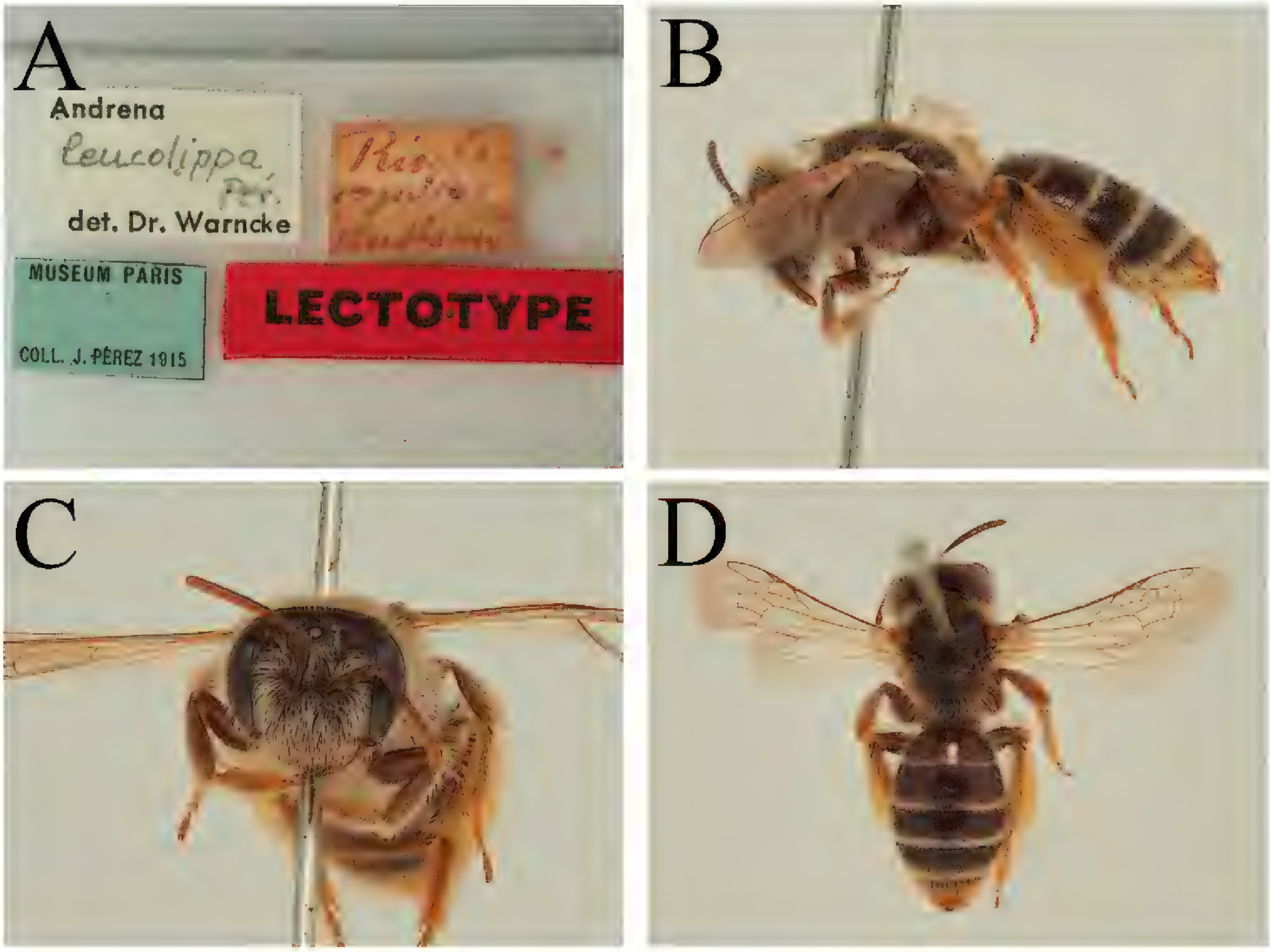

Figure 3. *Andrena* (*Chlorandrena*) *leucolippa* Pérez, 1895 female lectotype **A** label details **B** profile **C** face, frontal view **D** dorsal view.

assumed to be representative of true *A. leucolippa*. For now, the divergent Portuguese sequence is considered to be aberrant until it can be independently replicated. It is possible that this 'aberrant' sequence is a NUMT (nuclear sequences of mitochondrial origin) and represents amplification of nuclear DNA rather than mitochondrial. Since only a single sequence is available, and it is not possible to determine the nature of this sequence, no action is taken. It is not impossible that a third undescribed species is present, but without additional genetic data no further action is taken. Morphology supports the existence of only two species, and in order to fix the name *A. boyerella* on North African populations, a neotype is designated below from barcoded Moroccan material.

Andrena (*Chlorandrena*) *humilis* Imhoff, 1832 is the most widespread West Palaearctic *Chlorandrena*, and it is quite variable over its range. A broad species concept has been used as no consistent morphological differences can be found because of this variability. Sequences from Austria, Belgium, Finland, Germany, Portugal, and Spain formed a broad *A. humilis* clade (Fig. 2), though intraspecific variation was high at an average of 4.59% (range 0.00–8.33%). Specimens from Iberian mountain chains (Sistema Central, Sierra de Baza, Sierra Nevada) were the most strongly divergent, differing by 8.02–8.33% from specimens from Austria, Belgium, and Germany. However, multiple clades were found without clear geographic structuring. Therefore, a broad species concept is maintained

here, and this overall *A. humilis* clade has bootstrap support of 98. In Iberia, *A. humilis* forms a species pair with *A.* (*Chlorandrena*) *cinerea* Brullé, 1832. *Andrena cinerea* specimens from Morocco, Portugal, and Spain formed a distinct clade with low intraspecific variation of 0.77% (range 0.00–1.54%). This clade was strongly separated from the broad *A. humilis* clade by an average distance of 15.05% (range 13.89–15.74%). However, a single specimen from Balaguer in north-eastern Spain which was originally identified as *A. cinerea* diverged from both the broad *A. humilis* clade by 11.70% (range 11.11–12.65%) and *A. cinerea* by 12.35% (range 12.35–12.35%). As for the potentially aberrant specimen of *A. leucolippa*, it is not clear what this sequence represents, though it is not *A.* (*Chlorandrena*) *kamarti* Schmiedeknecht, 1900 from North Africa and Sicily as it also diverges from Moroccan *A. kamarti* sequences (to be published in the upcoming North African revision). It may also be a NUMT; it is unknown if certain *Andrena* subgenera are more likely to generate NUMTs, but *Chlorandrena* may potentially represent one such case, with difficult to interpret results generated in the study of the East Mediterranean fauna (G. Pisanty, unpublished data). More study using additional genetic markers is necessary to understand why two seemingly aberrant strong divergent sequences have been generated from Iberian *Chlorandrena* specimens.

Finally, the *taraxaci*-group (see Schwenninger 2015) formed a monophyletic clade, with *A.* (*Chlorandrena*) *rhenana* Stöckhert, 1930 clearly separated from *A.* (*Chlorandrena*) *taraxaci* Giraud, 1861 which has its western range limit in Central Europe. The taxonomic concepts of Schwenninger (2015) are therefore supported and followed.

Material examined. ***Andrena leucolippa*****:** **France:** Riscle [43.6564°N, -0.0894°W], 1♀, MNHN (lectotype; Fig. 3).

Subgenus *Didonia* Gribodo, 1894

Andrena (*Didonia*) *mucida* Kriechbaumer, 1873 is a highly unusual species. It is bivoltine, with the first generation seemingly specialising on *Muscari* (Asparagaceae) and the second generation specialising on genera from the former Dipsacaceae (now Caprifoliaceae) such as *Scabiosa*. This specialisation is associated with a morphological change, with females of the first generation possessing tibial scopae composed of simple hairs, and females of the second generation possessing tibial scopae composed of plumose hairs. There is the possibility that these generations may actually represent distinct species, as for putatively bivoltine taxa like *A.* (*Holandrena*) *decipiens* Schenck, 1861 that was found to consist of two taxa (Mandery et al. 2008). However, barcodes from females from the first and second generations from central and southern Spain show that this is not the case, with an average intraspecific genetic distance of 0.30% (range 0.15–0.46%; Fig. 4). The spring and summer generation individuals from Guadalajara were separated by 0.15%, strongly supporting the position that *A. mucida* is a bivoltine species displaying the currently unique trait of intergenerational variation in the structure of the pollen collecting hairs.

Additionally, *A.* (*Euandrena*) *solenopalpa* Benoist, 1945 was previously placed in the subgenus *Didonia* (Warncke 1968a). Genetic evidence instead places this taxon in the subgenus *Euandrena* (Bossert et al. 2022). This placement is a better fit, as

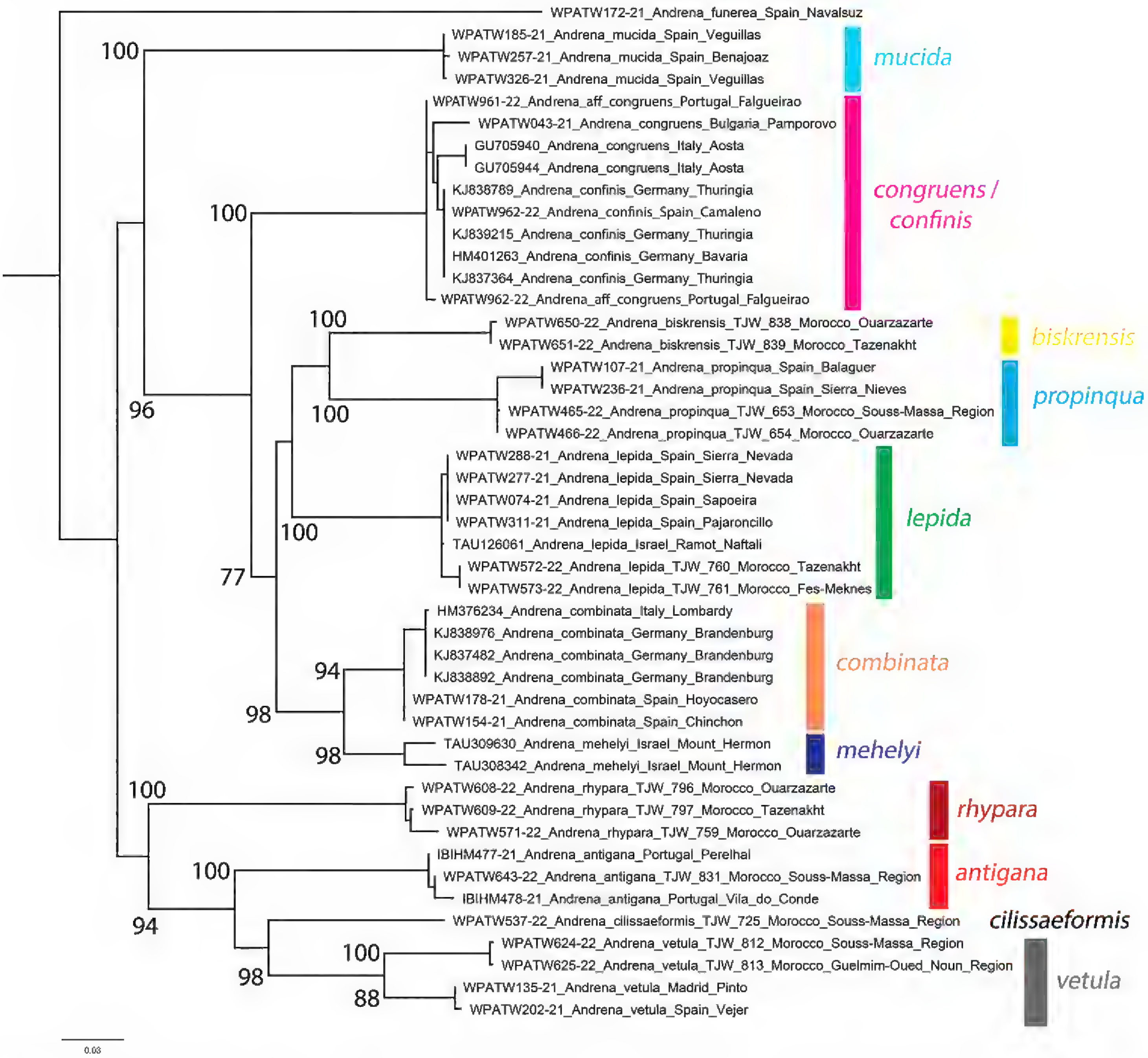

Figure 4. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Didonia* Gribodo, 1894 and *Simandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (*Nobandrena*) *funerea* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

A. solenopalpa has typical *Euandrena* foveae (narrow and narrowing further ventrally), the male A3 slightly exceeds the length of A4+5, and the process of the labrum is not so strongly thickened and elongate as in *A. mucida*; this simply represents convergence on a similar morphology. It is possible that the subgenus *Didonia* is monotypic, containing only *A. mucida*, but this requires additional study.

Material examined. ***Andrena mucida*:** Spain: Guadalajara, Veguillas, 2 km N, Barranco de la Isa, 17.v.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW185-21], on *Muscari* spp.; Málaga, Benaoján, Cueva del Hundidero, 3.vi.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW257-21], on *Scabiosa atropurpurea*; Guadalajara, Veguillas, CM-1006, 9.vii.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW326-21], on *Scabiosa atropurpurea*.

Subgenus *Euandrena* Hedicke, 1933

In comparison to the situation in the Eastern Mediterranean (Praz et al. 2019), Iberian *Euandrena* are comparatively well-resolved, with lower species diversity, fewer undescribed species, and clearer species boundaries. However, unrecognised montane species are present (Wood et al. 2021), and there are some problems related to the group of species lumped together under a broad *A. bicolor* Fabricius, 1775. This current work does not deal with the complex issue concerning the two clades of *A. bicolor* as identified by Praz et al. (2019), but instead with the status of material from southern Spain and North Africa. Material identified as *A. bicolor* s.l. from the Col du Zad in the Middle Atlas of Morocco at an altitude of 2100 m [WPATW387-22] and the southern slopes of the Sierra Nevada above Trevélez in Spain at an altitude of approximately 1800 m [WPATW368-21] fell close to *A. angustior* (Kirby, 1802) and far from *A. bicolor* s.l. (Fig. 5). The specimen from the Sierra Nevada was caught on the same *Campanula* (Campanulaceae) plant as specimen WPATW290-21 which falls into the *A. bicolor* s.l. clade. These two Spanish specimens are separated by a genetic distance of 9.80%, and clearly cannot be conspecific despite their strong morphological similarity.

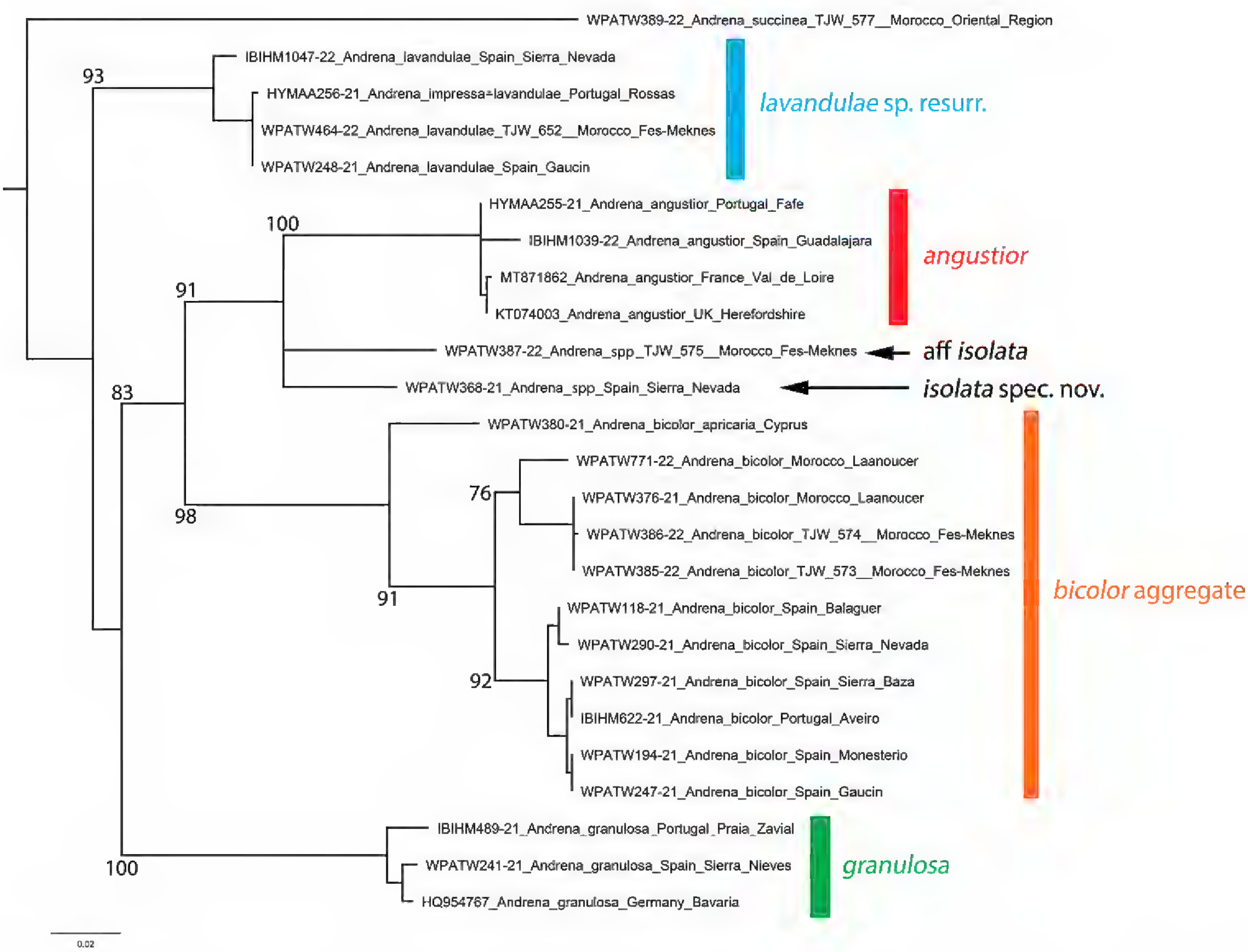

Figure 5. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Euandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena* (*Pruinosandrena*) *succinea* Dours, 1872 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

More broadly, the Sierra Nevada specimen was separated from the *A. bicolor* s.l. clade by an average genetic distance of 9.32% (range 7.95–9.80%) and the Moroccan specimen was separated from the *A. bicolor* s.l. clade by an average distance of 9.06% (range 8.50–9.80%). These two specimens were separated from each other by a distance of 4.99%. The species from the Sierra Nevada is described as new to science below, but the name to apply to the North African taxon (present also in Tunisia based on barcode data, Praz, in litt.) is complex and requires discussion. The nomenclatural and taxonomic status of *A. bicolor* s.l. will be resolved in a future revisionary work dedicated to the subgenus *Euandrena* at a West Palaearctic scale.

Andrena (*Euandrena*) *bicolor* and associated *Euandrena* species in North Africa

Euandrena specimens with black and orange pubescence can be found infrequently across north-western Africa. They have typically been referred to as *A. bicolor* in the literature, but two distinct taxa are present. One corresponds to *A. bicolor* s.l., but the other is clearly distinct genetically; morphologically it can be distinguished by the structure of the clypeus, with *A. bicolor* s.l. with the clypeus shiny between the punctures, whereas in the second taxon the puncture interspaces are shagreened and dull, and there is a weak longitudinal furrow, similar to what can be seen in species like *A.* (*Euandrena*) *angustior*, though more apically situated and occupying a shorter distance.

Warncke (1974) used subspecific concepts for dealing with *A. bicolor*, with two subspecies used for North African material – *A. b. oraniensis* Lepeletier, 1841 and *A. b. agraria* Warncke, 1974 (see also distribution maps in Gusenleitner and Schwarz 2002). However, the use of these names is not immediately straightforward. *Andrena oraniensis* Lepeletier, 1841 was described from Oran in northern Algeria (Lepeletier 1841) and is a confused and unclear taxon. In the MNHN collection, the type series cannot be located, and it may have been lost as many specimens have been moved between different boxes by past workers and curators. In the Pérez collection, there are long series of *Andrena* (*Melandrena*) *florentina* Magretti, 1883 that were identified by Pérez as *A. oraniensis*. Warncke (1967) noted this, but argued that this must be incorrect due to size, and instead placed the name in combination with *A. bicolor* as a subspecies found in North Africa. Warncke (1974) later authored the replacement name *A. bicolor agraria* Warncke, 1974 for *Andrena* (*Euandrena*) *nigriventris* Pérez, 1902 which was described from northern Algeria and Morocco (*locus typicus* Tangier, following lectotype designation) but which is a preoccupied name, nec. *Apis nigriventris* Gmelin, 1790 which is a synonym of *A.* (*Melandrena*) *nitida* (Müller, 1776). Warncke then used both *oraniensis* and *agraria* as subspecies, giving an overlapping distribution in Warncke (1974, e.g. both occurring at Oukaimeden in the High Atlas), but in his distribution maps (see Gusenleitner and Schwarz 2002) giving a non-overlapping distribution, with *oraniensis* more or less occurring only in Algeria and Tunisia and *agraria* occurring only in Morocco.

In the original description of *A. oraniensis*, Lepeletier (1841: 245) draws attention to the colour of the hairs on the hind legs. Specifically, he states that: "*cuisses des deux postérieures garnies des poils ferrugineux pales ; leurs jambes et leurs tarses à poils noirs en*

dessus, ferrugineux en dessous". This bicoloured tibial scopa (dark dorsally, ferruginous ventrally) does not correspond at all to members of the *A. bicolor* s.l. group which have uniformly orange tibial scopae. It does however correspond very well to the concept of *A. florentina* which has a distinctive bicoloured scopa, one of the characters that allows it separation from its sister taxon *A. bicolorata* (Rossi, 1790). Based on the identifications made by Pérez, who probably saw the original specimen in Lepeletier's collection and Lepeletier's original description, the position is taken that *A. oraniensis* cannot be a *Euandrena* taxon displaying the colour pattern of *A. bicolor* s.l. However, without a type, it is undesirable to make *A. oraniensis* the senior synonym for *A. florentina*. *Andrena oraniensis* is therefore declared a *nomen dubium* until such time as the original syntypic series can be located.

The next oldest available name from North Africa is *A. bicolor agraria*. Pérez (1902, as *A. nigriventris*) writes: "*Abdomen très luisant, particulièrement les depressions, que précèdent les bourrelets très prononcés*". This is suggestive, as the distinct North African taxon has strongly depressed tergal margins. However, barcoded *A. bicolor* s.l. from Morocco also show this character, so it is not diagnostic in and of itself. Examination of the lectotype specimen of *A. nigriventris* (designated by Warncke 1967; Fig. 6) shows that the clypeus is apically smooth and shing between the punctures (Fig. 6C), meaning that it cannot belong to the distinct taxon, and it remains a synonym of *A. bicolor*

Figure 6. *Andrena* (*Euandrena*) *nigriventris* Pérez, 1902 (nec. Gmelin, = *Andrena bicolor agraria* Warncke, 1974) female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

s.l. One additional name is available, that of *A.* (*Euandrena*) *fervida* Pérez, 1902, a taxon described from Algeria. The lectotype is in poor condition, lacking its metasoma (Fig. 7). Diagnosis is therefore challenging, but the clypeus is shiny between the punctures and it cannot be conspecific with the distinct North African taxon. The position of Warncke (1967) that this name is synonymous with *A. bicolor* s.l. is maintained. The distinct North African taxon would therefore appear to be undescribed. No taxonomic action is taken in the current work – further genetic data will either demonstrate a closer affinity with the specimen from the Sierra Nevada, in which case this name will be available to apply to North African populations, or these sequences will confirm its distinct nature, and it can be described. In any case, a name is required for the Iberian lineage which is unambiguously undescribed.

Material examined. ***Andrena bicolor*: Algeria:** Theniet El Had [35.8727°N, 2.0007°E] (1♀, MNHN (lectotype of *A. fervida*); **Morocco:** Tanger [35.7537°N, -5.7906°W], 1♀, MNHN (lectotype of *A. nigriventris* Pérez).

***Andrena* (*Euandrena*) *lavandulae* Pérez, 1902, sp. resurr.**

Andrena (*Euandrena*) *lavandulae* Pérez, 1902: 156 ♀♂ [France, lectotype by present designation: MNHN].

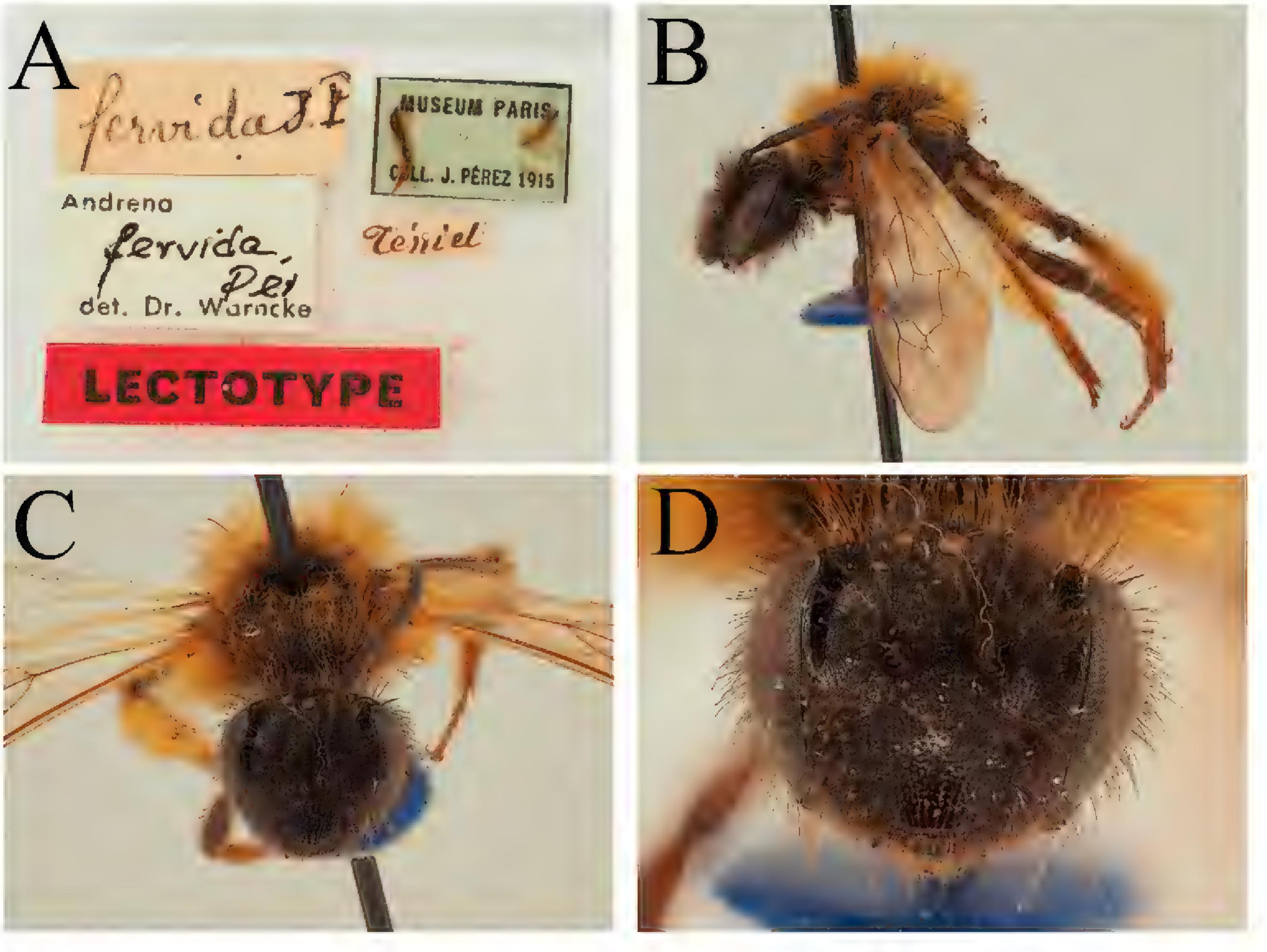

Figure 7. *Andrena* (*Euandrena*) *fervida* Pérez, 1902, female lectotype **A** label detail **B** profile **C** face, frontal view **D** face detail, frontal view.

Andrena (*Euandrena*) *angustior impressa* Warncke, 1967: 234, ♀♂ [Morocco: OÖLM, examined] syn. nov.

Remarks. Warncke (1967) synonymised *A. lavandulae* with *A. bicolor* without apparently inspecting the type. This is not explicitly clear in the text of Warncke (1967), but in this publication he typically reported lectotypes in the Paris collection when he designated them, and usually labelled paratypes as well, often taking a selection for his personal collection. There are no specimens of *A. lavandulae* in the Warncke collection, which combined with the lack of mention of a lectotype in Warncke (1967) leads me to believe that he did not inspect the type series. He then described *Andrena angustior impressa* Warncke, 1967 in the same publication, a taxon that was subsequently elevated to species status by Wood et al. (2021) based on genetic and morphological evidence.

In the MNHN collection, specimens of *A. lavandulae* are labelled as lectotype and paralectotype by Teunissen (August 1986; Fig. 8), but these designations were never published. The female specimen is therefore recognised here as a lectotype, by present designation. Examination of these specimens shows that they are clearly the same taxon as *A. impressa* and distinct from *A. bicolor*, with the weakly depressed, shagreened, and weakly shing tergal margins, the black terminal fringe and hairs flanking the pygidial plate, the intermixed light and dark hairs on the face, and in the male sex by the broadened gena (broader than the width of the compound eye). The lectotype comes from Banyuls-sur-Mer in the south-west of France, which falls within the distribution of the taxon as presented by Wood et al. (2021). Additional genetic sequences from Spain and Morocco closely match the Portuguese sequence of *A. impressa* presented by Wood et al. (2021), forming a well-supported clade (Fig. 5; bootstrap support of 93) that is distinct from both *A. angustior* and *A. bicolor*. *Andrena impressa* syn. nov. is therefore synonymised with *A. lavandulae* sp. resurr. The distribution is Morocco, Algeria, Portugal, Spain, and France (Wood et al. 2021).

Material examined. **France:** Banyuls [Banyuls-sur-Mer, 42.5658°N, 2.8658°E], 1♂, 1♀, MNHN (female lectotype, by present designation).

Subgenus *Graecandrena* Warncke, 1968

This subgenus is also species-poor in Iberia, containing only *A. impunctata* Pérez, 1895, *A. montarca* Warncke, 1975, *A. nebularia* Warncke, 1975, and *A. verticalis* Pérez, 1895. Two taxa are uncommonly collected in Iberia (*A. impunctata* and *A. montarca*). *Andrena nebularia* was considered to be endemic to Spain, but new collections in Morocco have demonstrated its presence in a small part of the Middle Atlas. Genetically, there is almost no differentiation, with the Moroccan specimens separated by 0.26% and 0.52% (Fig. 1).

Material examined. ***Andrena nebularia*:** **Morocco:** Fès-Meknès, Boulemane, 5 km SE, junction of R503 and N4, 1900 m, 19.v.2022, 2♀, leg. T.J. Wood, TJWC; Fès-Meknès, Boulemane, R503, 7 km SE of Boulemane, 1900 m, 1♂, 6♀, 22.v.2022, leg. T.J. Wood, TJWC; Fès-Meknès, Boulemane, R503, SE of Ait Karmosse, 1750 m, 22.v.2022, 1♂, leg. T.J. Wood, TJWC.

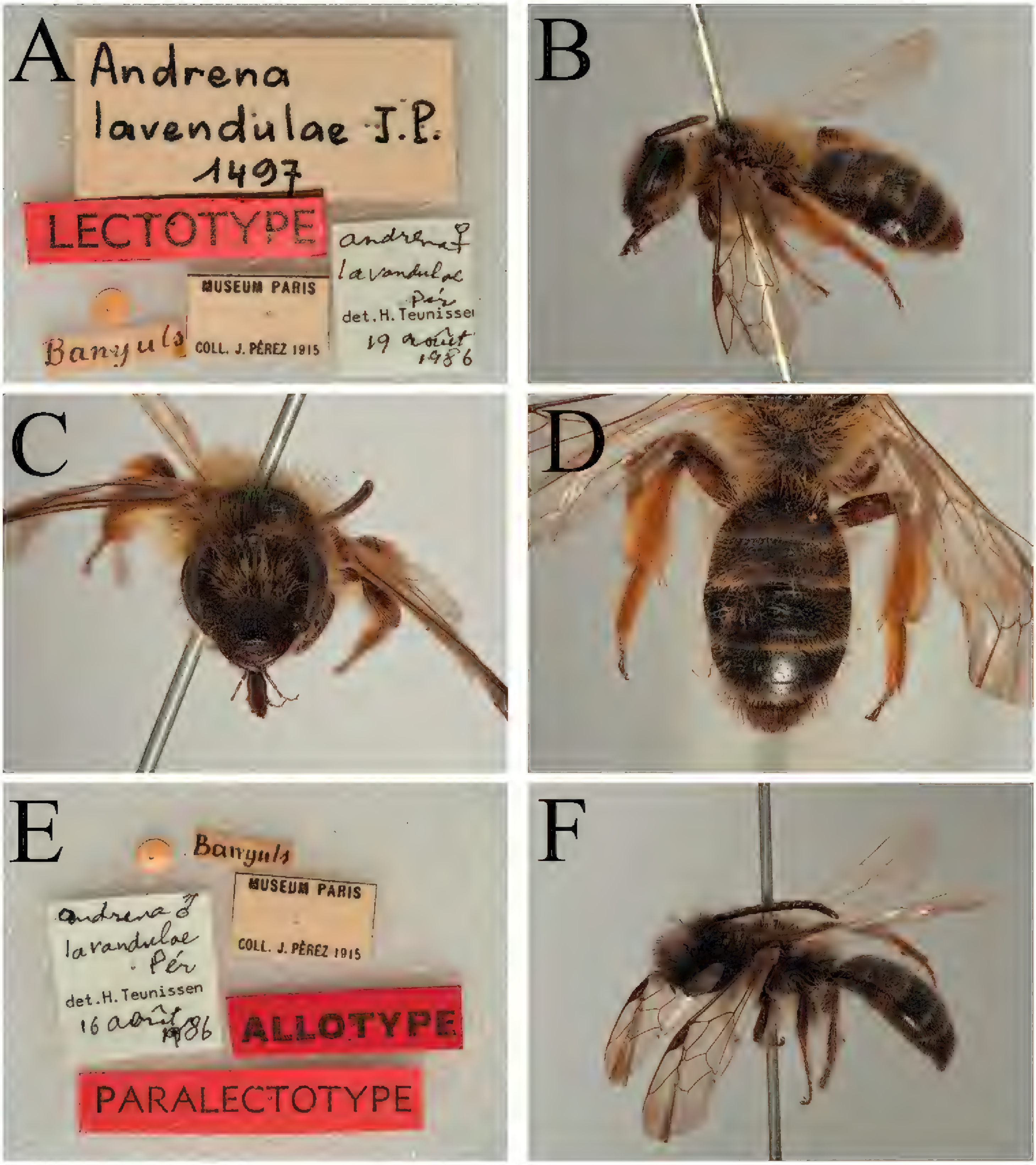

Figure 8. *Andrena* (*Euandrena*) *lavandulae* Pérez, 1902, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view; male syntype **E** label details **F** profile.

Subgenus *Melanapis* Cameron, 1902

Andrena (*Melanapis*) *fuscosa* Erichson, 1835

Andrena fuscosa was described from southern Spain by Erichson (1835). *Andrena fuscosa* has had a complicated taxonomic history, and has been described many times due to its variation in colouration and size (Gusenleitner and Schwarz 2002). Iberian genetic data are therefore of interest since the peninsula represents the *locus typicus*.

Iberian sequences were identical with each other, and closely matched sequences from Israel and India (the latter identified as *A.* (*Plastandrena*) *agilissima* Scopoli, 1770 but clearly misidentified; *Melanapis* was actually described as a genus based on material from India), being separated by an average of 1.53% (range 0.88–1.82%; Fig. 9). They were more clearly separated from Moroccan sequences, by an average of 5.43% (range 3.94–5.93%). Given the lack of morphological differences between North African and Iberian specimens, a broad interpretation of this species is taken here. Including all sequences together, average intraspecific distance is 3.14% (range 0.00–6.23%) which is considered to be acceptably small. Additional study is necessary to establish whether North African material is consistently distinct; the first nominally available name would be *A.* (*Melanapis*) *rutila* Spinola, 1838 which was described from Egypt.

Subgenus *Melandrena* Pérez, 1890

This subgenus is strongly derived within *Andrena*, but it shows substantial morphological variation that has led to the description of the subgenera *Hyperandrena* Pittioni, 1948 and *Zonandrena* Hedicke, 1933, both of which are now placed within an expanded *Melandrena*. There are several problems within this subgenus in an Iberian context.

Andrena (*Melandrena*) *morio* Brullé, 1832

Andrena (*Melandrena*) *morio* Brullé, 1832: 353, ♀♂ [Greece: MNHN, not examined].
Andrena (*Melandrena*) *hispania* Warncke, 1967: 212, ♀♂ [Spain: OÖLM, examined] syn. nov.

Remarks. *Andrena hispania* Warncke, 1967 was described from Algeciras in southern Spain. The identification characters given by Warncke are comparatively weak and rely on hair colour and the degree of infuscation of the wings, without mentioning definitive structural characters. Genetically, the three *A. hispania* sequences from Spain and Portugal mixed with *A. morio* sequences from Israel, Morocco, Portugal, Spain, Tunisia, and Turkey without forming a cluster, this group having bootstrap support of 100 (Fig. 10). Confusingly, additional sequences from Greece, Morocco, and Tunisia formed two sister groups to this clade. There is no clear geographic pattern, and so a broad *A. morio* concept is adopted, including *A. hispania* syn. nov. as a direct synonym of *A. morio*. Additional genetic data using more powerful techniques are required before an alternative taxonomic conclusion can be drawn. *Andrena morio* is known to be highly variable in its colouration, leading to a higher than average number of synonyms for an *Andrena* species (Gusenleitner and Schwarz 2002). *Andrena hispania* was classically thought of to have only a single generation in the spring, which may explain why its wings are less infuscate than *A. morio*, particularly in the summer generation of this species that can be noticeably darker than spring flying individuals.

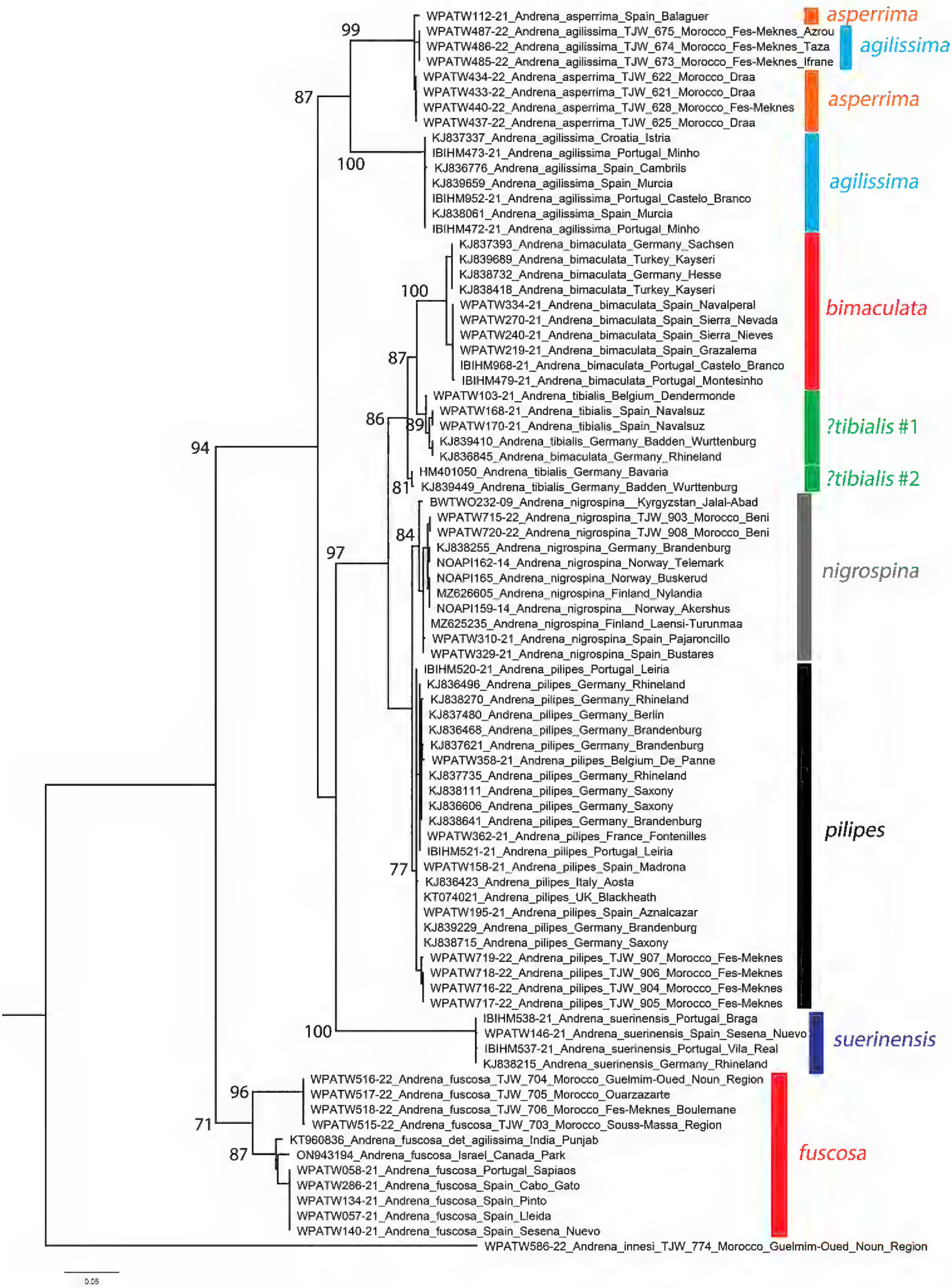

Figure 9. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Melanapis* Cameron, 1902, *Plastandrena* Hedicke, 1933, and *Suandrena* Warncke, 1968 based on the mitochondrial COI gene. *Andrena* (incertae sedis) *innesi* Gribodo, 1894 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

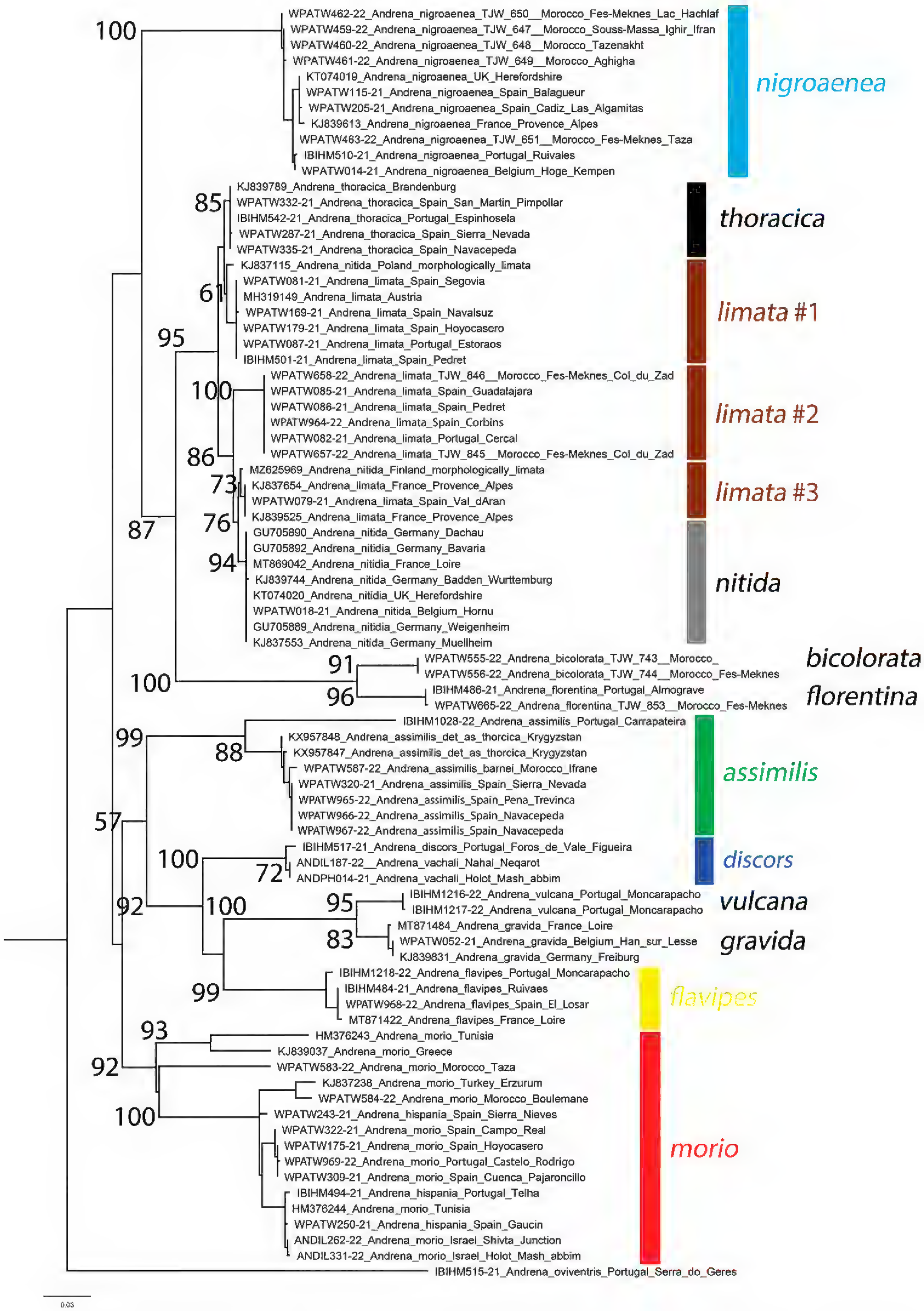

Figure 10. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Melandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

Andrena (*Melandrena*) *nitida* (Müller, 1776), *Andrena* (*Melandrena*) *thoracica* (Fabricius, 1775), and *Andrena* (*Melandrena*) *limata* Smith, 1853

Remarks. The specific differences between these taxa is unclear across southern Europe. In some northern countries, only two taxa are present (*A. nitida* and *A. thoracica*, e.g. the United Kingdom), with no introgression observed. *Andrena nitida* flies only in the spring, whereas *A. thoracica* is bivoltine, flying in both the spring and the summer. In Central Europe, *A. limata* can be found, this taxon also being bivoltine. Differentiation between the three taxa in Central Europe has often utilised hair colouration characters, as in this region the three taxa are separable with reference to the hairs on the sides of the mesosoma (light in *A. nitida* and *A. limata*, dark in *A. thoracica*) and the hairs of the face and the tibial scopal (light and dark in *A. nitida*, uniformly dark in *A. limata* and *A. thoracica*). There are additional characters such as the colour of the hind tibial spur and the density of the punctures T1, but these are less commonly referred to; both *A. nitida* and *A. limata* have dense punctures on T1 (separated by up to 1 puncture diameter), whereas they are more clearly spaced in *A. thoracica* (punctures separated by 1–2 puncture diameters). It is important to note that *A. limata* is a replacement name for *A. lucida* Lepeletier, 1841 nec. *A. lucida* Panzer, 1798 which is nominally a synonym of *A. bicolor* Fabricius, 1775 but this must be established (see section on subgenus *Euandrena*). *Andrena lucida* Lepeletier was described from 'France', without further details. I have not been able to inspect the type which should be in the MNHN collection, but which I could not locate.

The situation in southern Europe is much more challenging. In south-western Europe, *A. limata* becomes much darker, and therefore closely resembles the colour form of *A. thoracica*, with extensive black pubescence on the mesosoma laterally. This colour form was described as *A. limata mixtura* Warncke, 1967 (illustrated by Wood et al. 2020a). This form can be recognised by the dense punctures of T1, separating it from Iberia *A. thoracica*; the colour of the hind tibial spur is variable and of little consistent utility. Because of this variation, Warncke later adopted a much broader concept of *A. nitida*, with *A. nitida* s. str., *A. nitida limata*, and *A. nitida mixtura* (e.g. Warncke 1974). This position was not followed by Gusenleitner and Schwarz (2002) who followed a three distinct species interpretation (*nitida*, *limata* including *mixtura*, *thoracica*).

Analysis of barcodes does not provide clarity (Fig. 10). Whilst *A. thoracica* and *A. nitida* form reciprocally monophyletic clades, three different clades are formed for *A. limata*. There is no geographic pattern to these clades; clade #1 contains individuals from Austria, Poland (KJ837115; specimen identified as *A. nitida* but associated photograph on BOLD shows *A. limata* colour pattern), Spain, and Portugal; clade #2 contains individuals from Morocco, Spain, and Portugal; and clade #3 contains individuals from Finland (MZ625969; specimen identified as *A. nitida* but associated photograph on BOLD shows *A. limata* colour pattern), France, and Spain. Confusingly, sequences IBIHM501-21 and WPATW086-21 come from two different female specimens collected from the same field near Pedret i Marzà in north-eastern Spain. As Iberian individuals fall into three of these clades and the power of COI analysis is

clearly insufficient to deal with potential hybridisation and introgression, no further action can be taken on the basis of these results. A dedicated study using more powerful genetic markers is necessary to resolve this issue. For now, I maintain the position of Gusenleitner and Schwarz (2002) in that there are three species in this group (*nitida*, *limata* including *mixtura*, and *thoracica*). It will probably be necessary for a future study to designate a neotype for *A. limata* if Lepeletier's original specimens cannot be definitively located.

***Andrena* (*Melandrena*) *discors* Erichson, 1841**

Andrena (*Melandrena*) *discors* Erichson, 1841: 192, ♀ [Algeria: ZMHB, examined].
Andrena (*Melandrena*) *creberrima* Pérez, 1895: 46, ♀♂ [Algeria: MNHN, examined] syn. nov.
Andrena (*Melandrena*) *vachali* Pérez, 1895: ♀ [Tunisia, lectotype by present designation: MNHN] syn. nov.
Andrena (*Melandrena*) *bodemeyeri* Benoist, 1969: 246, ♀ [Tunisia: MNHN, examined].

Remarks. There has been extensive confusion between *A. discors* and *A. creberrima*. Erichson (1841) described *A. discors* from Algeria; a specimen is preserved in the ZMHB collection which may be automatically the holotype, but this is ambiguous as it is unclear if Erichson described the species from multiple specimens (Fig. 11). In any case, the specimen is a syntype, and Erichson described the species only in the female sex. The specimen conforms to the classical concept of the species, having the typical features of the former members of the subgenus *Zonandrena*, i.e. a clypeus with punctures forming a pattern of weak longitudinal channels. The pubescence of the face is black (Fig. 11C), and there are numerous intermixed dark hairs on the scutum (Fig. 11D). The tibial scopae are orange (Fig. 11E), and there are weak indications of light tergal hair bands but these are degraded and scarcely visible (Fig. 11F). Warncke (1974) gave numerous localities for *A. discors* from Morocco, Algeria, and Tunisia. He listed *A.* aff *discors* from Madrid based on two specimens (Warncke 1976), but later discarded these records, giving only two points in southern Spain in his distribution maps in addition to the points from north-western Africa (Gusenleitner and Schwarz 2002). I have examined 14 female and six male specimens of *A. discors*, all from southern parts of Portugal and Spain (Algarve, Alto Alentejo, Cádiz, Huelva, Málaga, Sevilla), where it is active from late February to April.

The situation is confused due to the status of two additional taxa described by Pérez, *A.* (*Melandrena*) *creberrima* Pérez, 1895 and *A.* (*Melandrena*) *vachali* Pérez, 1895. *Andrena creberrima* was described from Algeria like *A. discors*. Warncke (1967) designated a lectotype for *A. creberrima* (Fig. 12), but did not understand the concept of this species, listing only the type locality of Bône in Warncke (1974). He later gave a distribution map of Algeria (the holotype point), Italy, and Greece (Crete). Examination of the lectotype shows that the specimen is slightly paler than the type of *A. discors*, with fewer dark intermixed hairs on the scutum (Fig. 12B), and the tergal hair bands

Figure 11. *Andrena* (*Melandrena*) *discors* Erichson, 1841, female holotype/syntype **A** label details **B** profile **C** face, frontal view **D** scutum, dorsolateral view **E** tibial scopa, profile view **F** terga, dorsal view.

in better condition and therefore slightly more pronounced (Fig. 12D). This can be contrasted with the type of *A.* (*Melandrena*) *bodemeyeri* (Fig. 13; known synonym of *A. discors*, see Warncke 1967) which is comparatively dark. This kind of variation in hair colour is typical for the subgenus *Melandrena*, and has led to the large number of synonymous names being described, for example for *A.* (*Melandrena*) *flavipes* Panzer, 1799.

Grouping *A. creberrima* under *A. discors* is straightforward. The problem comes with *A. vachali* which was classically considered to be distinct from *A. discors* and with a greater range extending from the Canary Islands to southern Israel (Gusenleitner

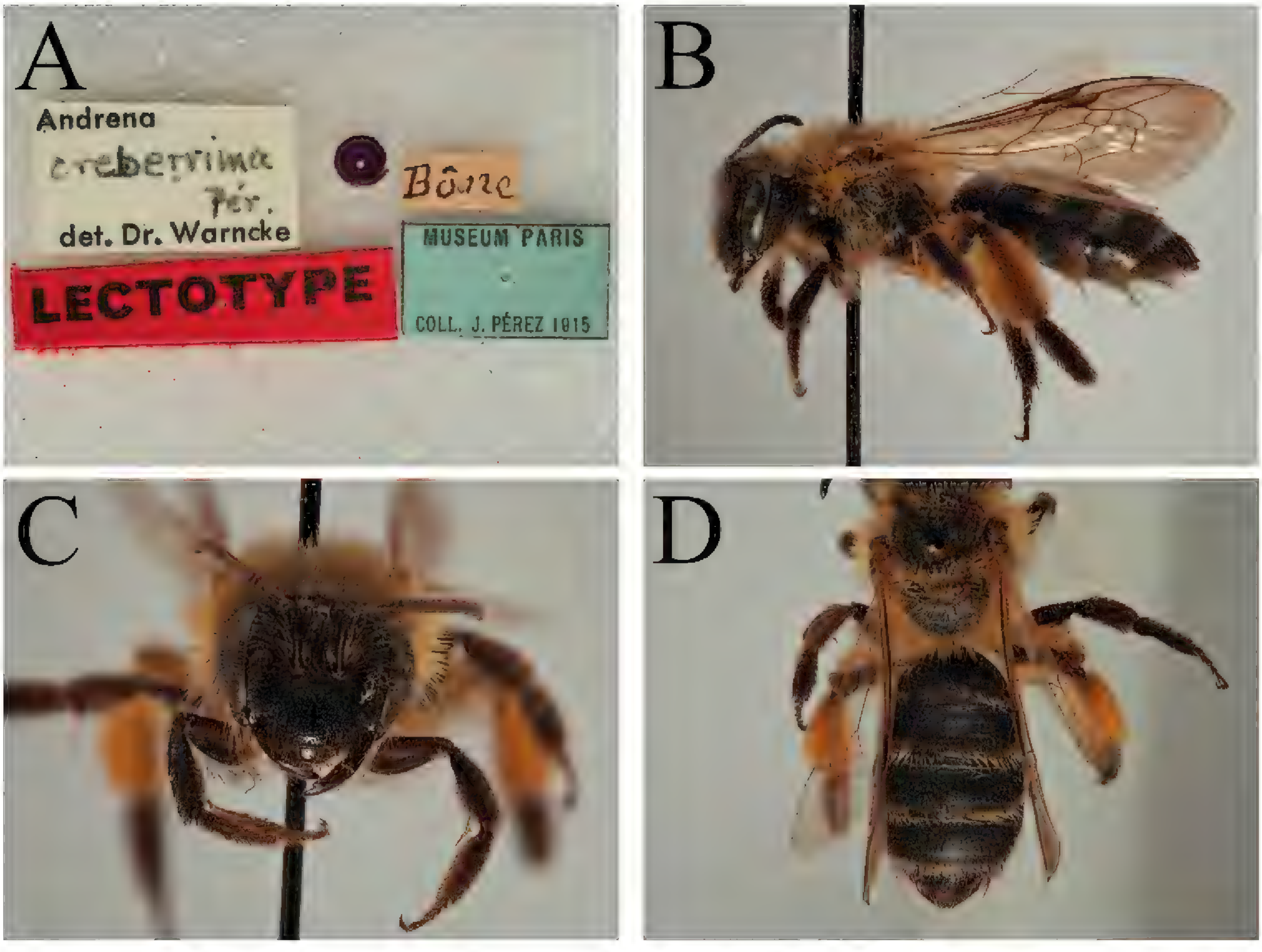

Figure 12. *Andrena* (*Melandrena*) *creberrima* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

and Schwarz 2002). Moreover, type material for *A. vachali* has not actually been designated, as Warncke (1967) could not find material in the MNHN collection. Examination of the MNHN showed several specimens of *A. vachali* in the Vachal collection from Foum Tatahouine [Tataouine, Tunisia] labelled "*Andrena vachali type Pérez*" in the handwriting of Vachal (Fig. 14). One specimen was labelled as a lectotype with a handwritten '*A. vachali*' determination label by H. Teunissen (Fig. 14A), but this designation was never published. Pérez (1895) did not mention the collection locality, and Warncke (1967) indicated that the species was described from Algeria. However, Gusenleitner and Schwarz (2002) give the *locus typicus* as Tunisia. Examination of the catalogue of Pérez did not reveal an entry for *A. vachali*, as is often the case, either because Pérez did not write one, or because the information is hidden under a name that differs from the published name (see below for the case of *A.* (*Plastandrena*) *asperrima* Pérez, 1895). It is therefore very difficult to know the type locality with certainty. However, on the basis that the MNHN specimens are labelled as 'type' by Vachal, they were present in his collection, and the species was named after Vachal, the position is taken that these represent genuine syntypes. The female specimen labelled as 'type' by Vachal is chosen as a lectotype, by present designation. Morphologically, it corresponds to the concept of *A. vachali*, with black pubescence on the face and mesepis-

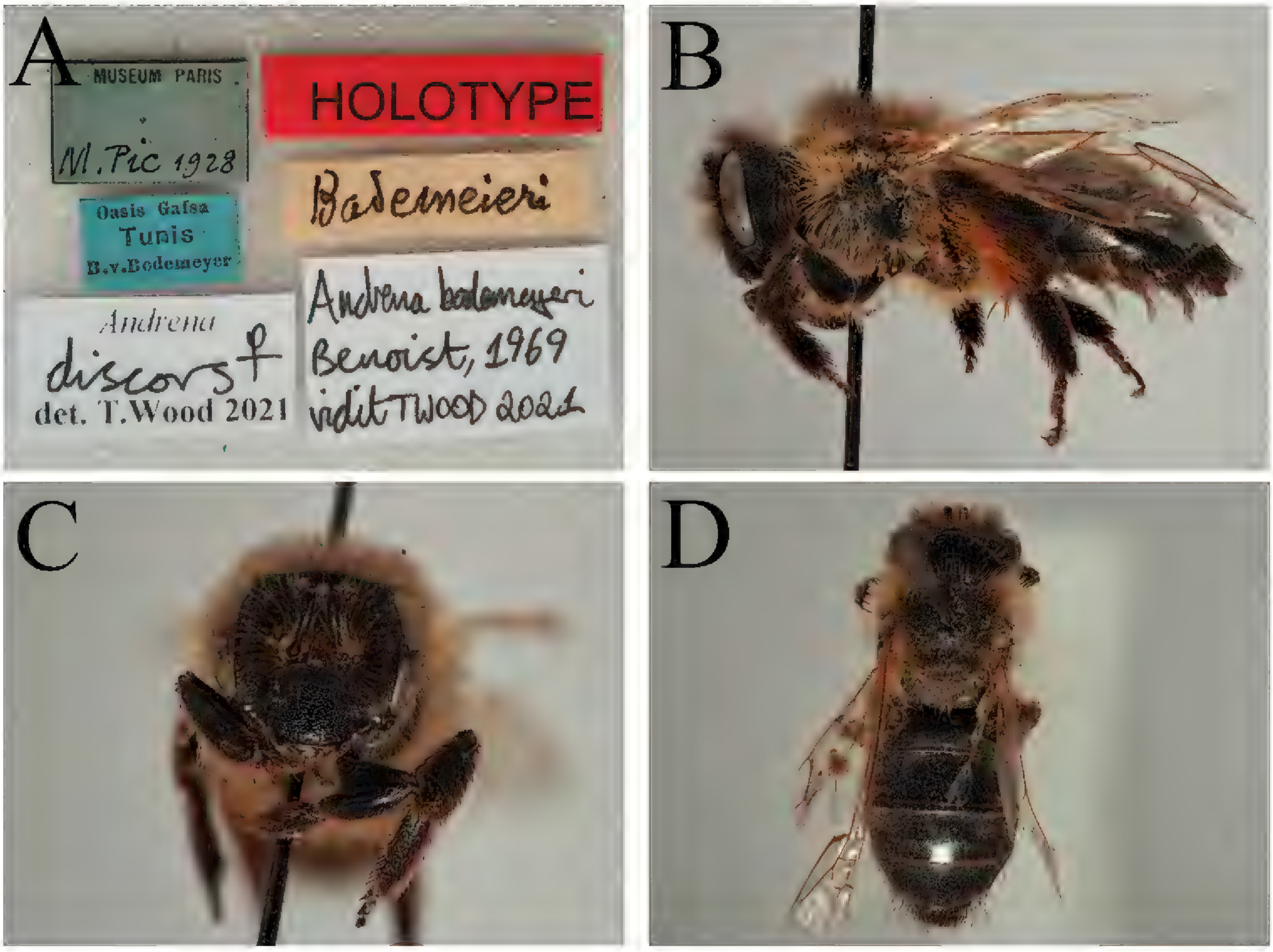

Figure 13. *Andrena* (*Melandrena*) *bodenmeyeri* Benoist, 1969, female holotype **A** label details **B** profile **C** face, frontal view **D** dorsal view.

ternum, with reddish-brown pubescence on the remaining parts of the mesosoma, and with predominantly reddish-brown tibial scopae, though this specimen shows some darker hairs dorsally (c.f. Fig. 13D); specimens of *A. vachali* can be found with entirely orange-red tibial scopae. Comparison of sequences from *A. discors* from southern Portugal and two *A. vachali* from southern Israel show a very small difference of 0.91% (range 0.91–0.91%; Fig. 10). These three specimens group together and have posterior support of 100, and are clearly separated from the three other former *Zonandrena* species that group together in this clade, namely *A. flavipes*, *A.* (*Melandrena*) *gravida* Imhoff, 1832, and *A.* (*Melandrena*) *vulcana* Dours, 1873.

Taking a step back, the differentiation between *A. creberrima*, *A. discors*, and *A. vachali* has almost always been based on colouration, with *A. discors* the darkest, *A. vachali* the lightest, and *A. creberrima* somewhat intermediate. Males are generally rarer in collections; taken together, I have examined 215 female specimens, but only 73 male specimens of this *discors-creberrima-vachali* group. However, examination of males has led me to the conclusion that there are no apparent differences in the males of *A. creberrima*, *A. discors*, and *A. vachali*, and indeed the male of only one of these nominal taxa was actually originally described. All have white hairs over the majority of the face with clear black hairs laterally along the inner margins of the compound eyes,

Figure 14. *Andrena* (*Melandrena*) *vachali* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

a genital capsule that is typical of the former *Zonandrena* with the dorsal surface of the gonocoxae with granular shagreen, with the penis valves moderately broad, and without an emargination in the outer margins of the gonostyli (Fig. 15). Indeed, the genital capsule of a syntype of *A. creberrima* (Fig. 15B), the barcoded *A. discors* from southern Portugal [IBIHM517-21] (Fig. 15C), and *A. vachali* specimens from Morocco have identical genital capsules (Fig. 15D). Moreover, numerous 'aberrant' female individuals can be found across this range with more or less pronounced tergal hair bands and variably dark or light pubescence, particularly in Crete where individuals corresponding in different ways to the concepts of *A. creberrima*, *A. discors*, and *A. vachali* can be found.

Based on this colour variation, the lack of variation in the male genital capsule, the unclear and overlapping distributions given by Warncke (*A. creberrima* and *A. vachali* both reported from Crete, *A. creberrima* and *A. discors* both reported from Algeria), and the very low genetic distance between Portuguese and Israeli specimens, both *A. creberrima* syn. nov. and *A. vachali* syn. nov. are synonymised with *A. discors*. This resolves this long-running confusion as to the correct name and identity of this taxon (Baldock et al. 2018; Wood et al. 2020a).

Distribution. Portugal, Spain (Canary Islands, mainland), Morocco, Algeria, Tunisia, Italy, Malta, Libya, Greece (Crete), Egypt, Israel, Jordan.

Figure 15. *Andrena* (*Melandrena*) *creberrima* Pérez, 1895, male syntype **A** label details **B** male genital capsule; *Andrena* (*Melandrena*) *discors* Erichson, 1841 **C** male genital capsule; *Andrena* (*Melandrena*) *vachali* Pérez, 1895 **D** male genital capsule.

Material examined (illustrative). **Algeria:** label information illegible, possibly '*Bone*' [= Annaba], 1♀, ZMHB (holotype/syntype of *A. discors*); Bône [=Annaba, 36.9092°N, 7.7264°E], 1♀, MNHN (lectotype of *A. creberrima*); Alger, Birmandreis [Bir Mourad Raïs], 24.iii.-30.iv.1910, 1♂, 1♀, leg. J. Bequaert, ZMHB; **Greece:** Krete, Anidri b. Paleochora, 200 m, 31.iii.2002, 1♀, leg. A. Müller, AMC; Krete, Palaeochora, 0–50 m, 29.iii.2002, 5♀, leg. A. Müller, AMC; Kreta, Kavalos [Kavallos], 21.v.1986, 1♀, leg. Brande, OÖLM; Crete, Dept. Heraklion, Moulia, S. of Aghia Varvara, 26.iv.1973, 1♀, leg. v. Ooststroom, RMNH; **Italy:** Lazio, Roma, Via Falcognana, 8.iv.1990, 1♀, leg. G.G.M. Schulten, RMNH; Roma, Via Falcognana, 15.iv.1993, 1♀, leg. G.G.M. Schulten, RMNH; **Israel:** Negev, 15 km S of Be'er Sheva, 31.iii.1988, 2♀, leg. R. Leys, RMNH; **Jordan:** Petra, 800 m, 28.ii.-4.iii.1986, 1♂, 2♀, leg. K.M. Guichard, NHMUK; **Malta:** Buskett [woodlands, Had-Dingli], 7.iii.2018, 1♀, M. Balzan Colln.; **Morocco:** Drâa-Tafilalet, Tazenakht, Anezal, 5 km NE Ait Igga, 21.iv.2022, 1♂, 4♀, leg. T.J. Wood, TJWC; Souss-Massa, R105, Tizirt, 8 km N, Ighir Ifran env., 12.iii.2022, 1♂, 1♀, leg. T.J. Wood, TJWC; **Portugal:** Foros de Vale Figueira, Montemor-o-Novo, 20.iii.2019, 1♂, leg. T.J. Wood, TJWC; Montemor-o-novo, Foros de Vale de Figuera, 24.iv.2011, 1♀, leg. A. Albernaz-Valente,

TJWC; **Spain:** Canary Islands, Lanzarote, Haria, 6.ii.1979, 1♂, leg. Ellis & Simon-Thomas, RMNH; Bollullos Par del Condado (Huelva), 160 m, 28.iii.2009, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Puerto de Gáliz, P.N. Alcornocales (Cádiz), 425 m, 28.iv.2007, 1♀, leg. F.J. Ortiz-Sánchez, FJOS; Cádiz, Zahara de los Atunes, 12.iii.1977, 1♀, leg. Madey, NHMUK; **Tunisia:** Foum Tatahouine [32.9361°N, 10.4458°E], 1♀, MNHN (lectotype of *A. vachali*, by present designation); Oasis Gafsa [34.4350°N, 8.7678°E], 1928, 1♀, leg. B. v. Bodemeyer, MNHN (holotype of *A. bodemeyeri*); Fritissa, 17–19. iv.1983, 1♀, TJWC.

Subgenus *Micrandrena* Ashmead, 1899

This is by far the most species-rich subgenus in Iberia, containing 37 species. Pisanty et al. (2022b) took the decision to synonymise the subgenera *Distandrena* Warncke, 1968, *Fumandrena* Warncke, 1975, and *Proxiandrena* Schmid-Egger, 2005 with a broad concept of *Micrandrena*, as morphological differences such as the shape of the foveae, propodeal triangle, and presence or absence of striations on the clypeus are inconsistent and insufficient to allow unambiguous differentiation between the groups, as well as lacking phylogenetic support. This broad *Micrandrena* definition is followed here.

Andrena (*Micrandrena*) *obsoleta* Pérez, 1895 and *Andrena* (*Micrandrena*) *mariana* Warncke, 1968 sensu lato

The treatment of *A. obsoleta* has a long and confused history that has caused many problems. Warncke (1967) designated a female lectotype from Babor in northern Algeria (Fig. 16). However, this lectotype designation is incorrect. In the catalogue of Pérez, under entry 1506 (p. 214), Pérez writes: "*Sicile,* ♀ *- M'pellier* ♀. *– Tebessa, avril,* ♀. *– Biskra, mars,* 3♀, *rares. – Bône,* ♀. *– Marseille,* ♂. *- Bône,* 27/iv ♂♀ *in cop. Souci et autres* [illegible – presumably a type of flower]". Babor is not mentioned, and so Warncke's lectotype designation is rejected. Examination of specimens labelled as *obsoleta* by Pérez from the localities indicated shows that they belong to a different taxon to that of Warncke's false lectotype. Warncke's false lectotype is a female *Distandrena* (=*Micrandrena*) with a clearly striate clypeus, and T1 is polished. This conforms to the concept of *A.* (*Micrandrena*) *nitidula* Pérez, 1903, and indeed Warncke (1967) synonymised *A. nitidula* with *A. obsoleta*. Only female specimens of *A. obsoleta* from Bône [=Annaba] in northern Algeria could be found in the Pérez collection, and almost all were in very poor condition, missing their metasomas. A single female from Bône was however in good condition, and it is here designated as a new lectotype (Fig. 17). This new lectotype specimen (i.e. the true *A. obsoleta*) morphologically falls within the *A.* (*Micrandrena*) *mariana* Warncke, 1968 complex within the former *Distandrena*, as it lacks striations on the clypeus. The larger *A.* (*Micrandrena*) *merimna* Saunders, 1908 can be excluded as this species has a very long A3 that clearly exceeds the length of A4+5, whereas members of the *A. mariana* complex have A3 at most slightly exceeding A4+5, A4 and A5 are sub-quadratic and slightly shorter than wide, A6–12 are as long as wide.

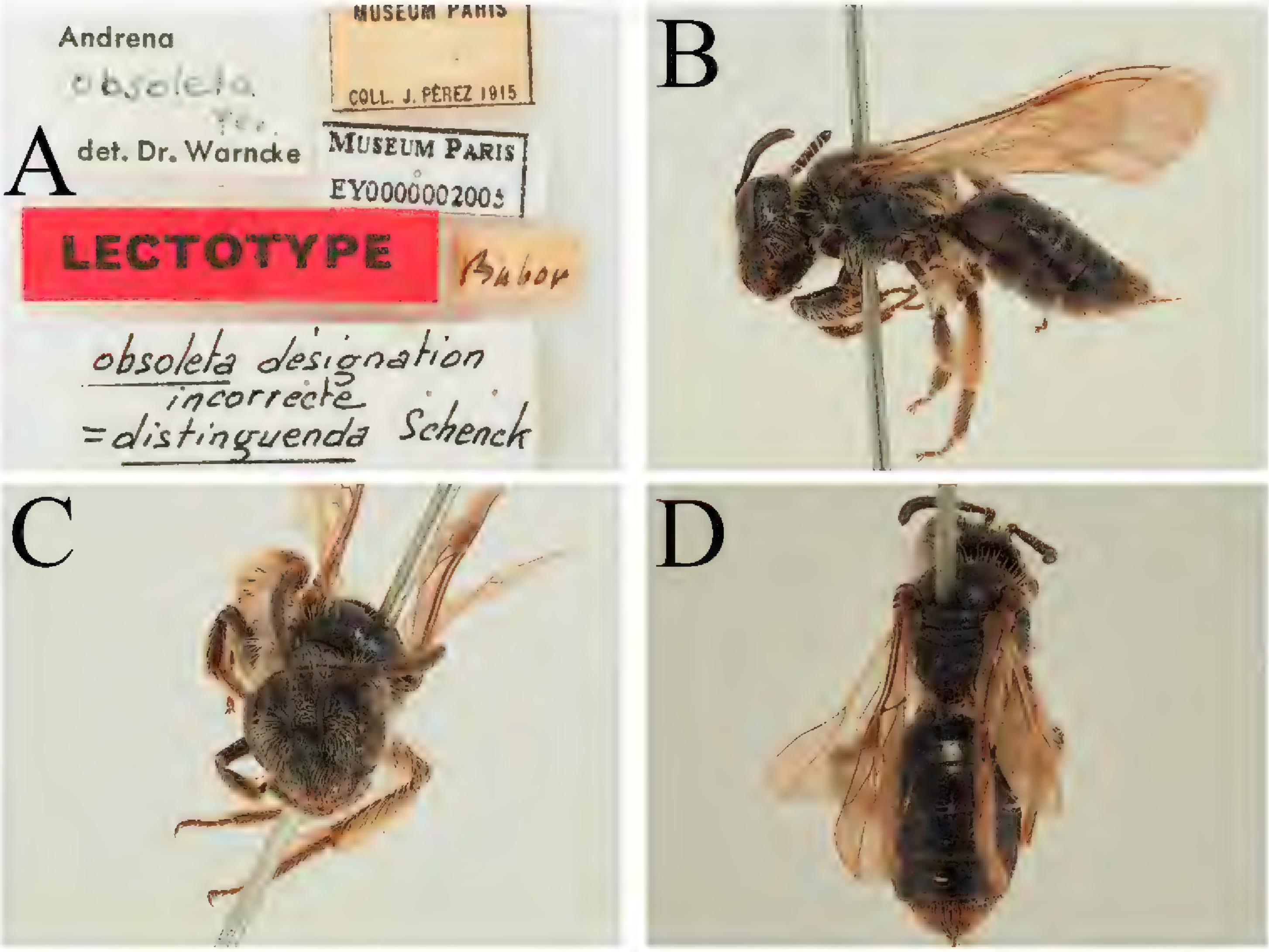

Figure 16. *Andrena* (*Micrandrena*) *obsoleta* Pérez, 1895, false female lectotype, =*Andrena* (*Micrandrena*) *nitidula* Pérez, 1903 **A** label details **B** profile **C** face, frontal view **D** dorsal view.

Warncke described *A. mariana* s. str. from the island of Fuerteventura in the Canary Islands, stating that the species could potentially be found in Morocco (Warncke 1968b). He then described five subspecies in subsequent publications (Warncke 1974, 1975a): *A. m. mica* Warncke, 1974, *A. m. leptura* Warncke, 1974, *A. m. solda* Warncke, 1974, *A. m. alma* Warncke, 1975, and *A. m. tenostra* Warncke, 1975. For North African taxa, Warncke (1974) described *A. mariana solda* from Morocco (Tangier) and Algeria (Algiers, including Husseyn-Dey [Hussein Dey] the *locus typicus*, Constantine, Bone, Blida) and Tunisia (Carthago), and noted that this species corresponds to the *Andrena* forms from Bone identified as *iota*, *kappa*, and *lambda* by Saunders (1908), though this is clearly wrong for *lambda* as the genital capsule illustrated by Saunders shows *A.* (*Micrandrena*) *djelfensis* Pérez, 1895. The *A. mariana solda* taxon differs from *A. mariana* s. str. in the female sex by the darker tergal margins, the darker antennae, and the more extensively shagreened clypeus. Warncke (1974) described *A. mariana mica* from southern Algeria (*locus typicus* Ghardaia) and Morocco, giving it a more arid distribution. It also differs from *A. mariana* s. str. in the female sex by the darker tergal margins and darker antennae, but the clypeus is more extensively shiny than in *A. mariana solda*, and the nervulus is said to be more antefurcal. *Andrena m. leptura* is a more eastern taxon, being described from Libya and Egypt, and having a broader process of the labrum than any of these species.

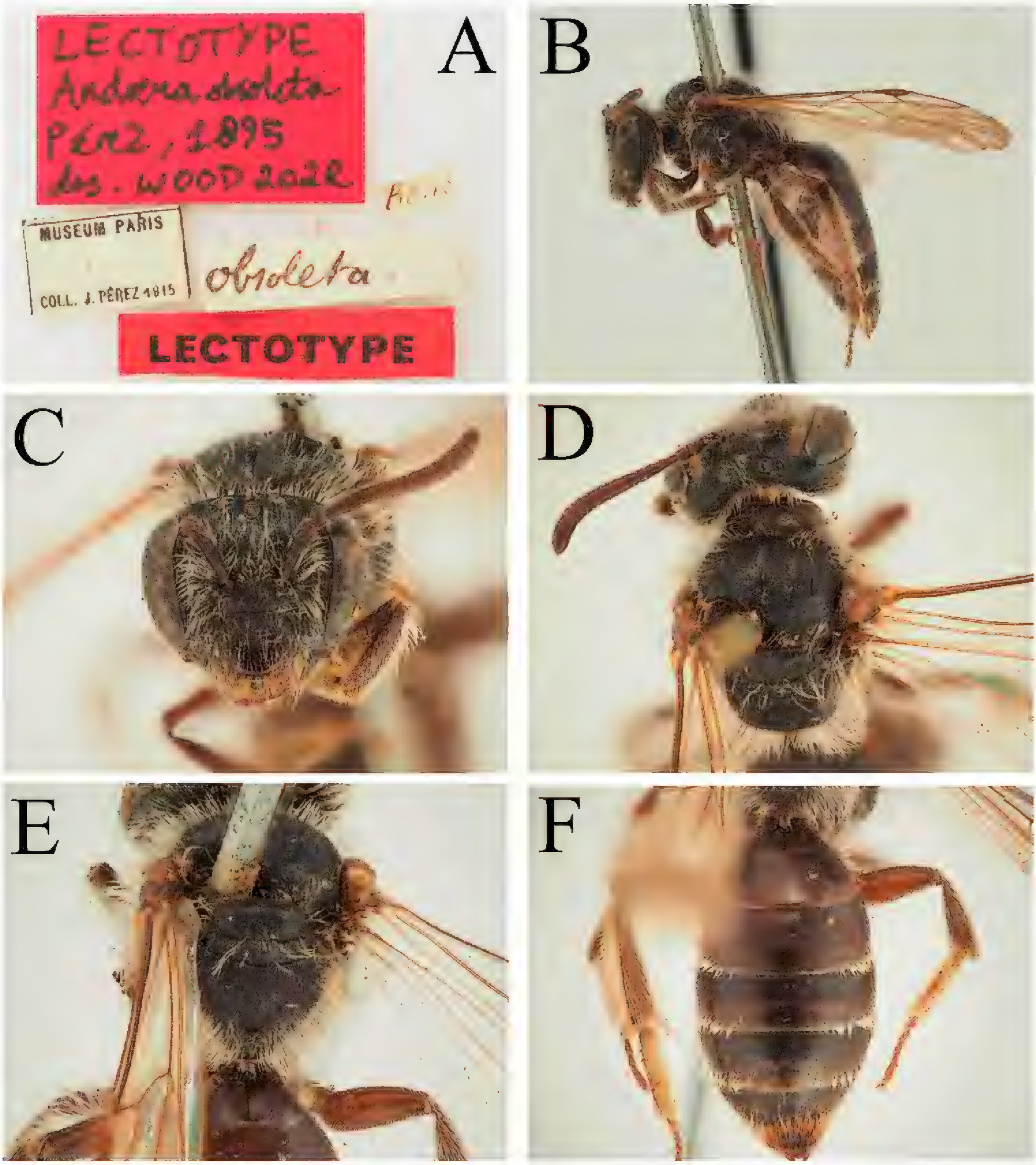

Figure 17. *Andrena* (*Micrandrena*) *obsoleta* Pérez, 1895, true female lectotype **A** label details **B** profile **C** face, frontal view **D** scutum, dorsal view **E** propodeal triangle, dorsal view **F** terga, dorsal view.

Examination of *A. mariana solda* material reveals that it is conspecific with the newly designated lectotype of *A. obsoleta* and is synonymised with it syn. nov. As identified by Warncke, the taxon has a wide distribution across Mediterranean parts of Morocco, Algeria, and Tunisia (Warncke 1974, as *A. m. solda*). Pérez's reference to specimens from France indicates that his original syntypic series would have been polytypic, or he may have changed his mind between writing this catalogue entry and his 1895 publication, or even after this point. Warncke (1974: 40) indicated that *A. m. solda* is present in Sicily which is supported by a newly examined specimen (see below),

though he did not designate any Italian specimens as paratypes. As no specimens from France labelled as *obsoleta* could be found in Pérez collection, the conservative position is taken here that this species does not occur in France. The implications for Warncke's misinterpretation of *A. obsoleta* are discussed below.

As *A. mariana solda* is actually a synonym of a valid species that was described prior to *A.* (*Micrandrena*) *mariana* s. str., this has implications for the species-status of the other taxa lumped under *A. mariana* by Warncke. Genetic sequences were available for *A. mariana mica* Warncke, 1974 from southern Morocco, *A. mariana* s. str. from south-western Morocco, and *A. mariana alma* Warncke, 1975 from Portugal (*locus typicus* near Córdoba, southern Spain; Fig. 18). Contrary to the position of Warncke (1968b), examination of material from Morocco, Algeria, and Tunisia shows that *A. mariana* is actually widely distributed across this region, predominantly in southern, more arid areas. Genetically, *A. mariana* s. str. was more closely related to *A.* (*Micrandrena*) *abjecta* Pérez, 1895, separated by an average genetic distance of 5.55% (range 5.49–5.61%), and was strongly separated from *A. m. mica* by 12.73% (range 12.50–12.95%) and *A. m. alma* by 10.94% (range 10.65–11.39%). *Andrena abjecta* + *A. mariana* s. str. therefore formed a clade with bootstrap support of 99. *Andrena m. mica* and *A. m. alma* formed a clade, but were strongly separated from each other by 11.26% (range 10.97–11.41%). The conclusion therefore is that each of these taxa is distinct, and so *A. mica* stat. nov. and *A. alma* stat. nov. are raised to species status. Morphologically, all three taxa can clearly be separated by the structure of the female clypeus, the colour of the antennae, the extent of lightening on the tergal margins, the strength of the scutal punctures, and the shape of the process of the labrum.

Warncke described two further subspecies of *A. mariana*: *A. mariana leptura* from Egypt and *A. mariana tenostra* from south-eastern Spain, the latter specifically from a single female specimen from Villajoyosa in the province of Alicante, then listing additional specimens from Almería and Murcia (Warncke 1976). The status of *A. mariana leptura* will be dealt with in a future publication, as its exact species concept and its eastern and western limits are unclear, though it will be a valid species as it clearly differs from *A. mariana* s. str.; its relationship with *A. mariana* s.l. specimens from southern Israel must also be clarified (Pisanty, in litt.). In Iberia, *A. m. tenostra* is very poorly known. The distinguishing features given by Warncke (1975a) are that the process of the labrum is narrowly trapezoidal and that the clypeus is arched and somewhat flattened in the middle, in contrast to *A. alma* where the clypeus is largely flattened. Additional female specimens were found in Granada which highlight a difference not noted by Warncke, which is that the scutellum is polished and shiny, whereas it is dull in *A. alma*, and more broadly the scutal punctures are less strongly pronounced. Given that subtle differences within this group represent large genetic differentiation, *A. tenostra* stat. nov. is raised to species status.

Finally, a number of specimens were found in the very south of Spain (Málaga, Sevilla) which show a morphology very close to that of *A. mica*. However, ecologically this does not make sense as *A. mica* is not known from the more humid and Mediterranean areas north of the Atlas Mountains. Examination of these specimens shows that A3 is much longer than A4+5, whereas it is as long as A4+5 in *A. mica*. These specimens probably represent an additional undescribed species in the *A. mariana* complex, but

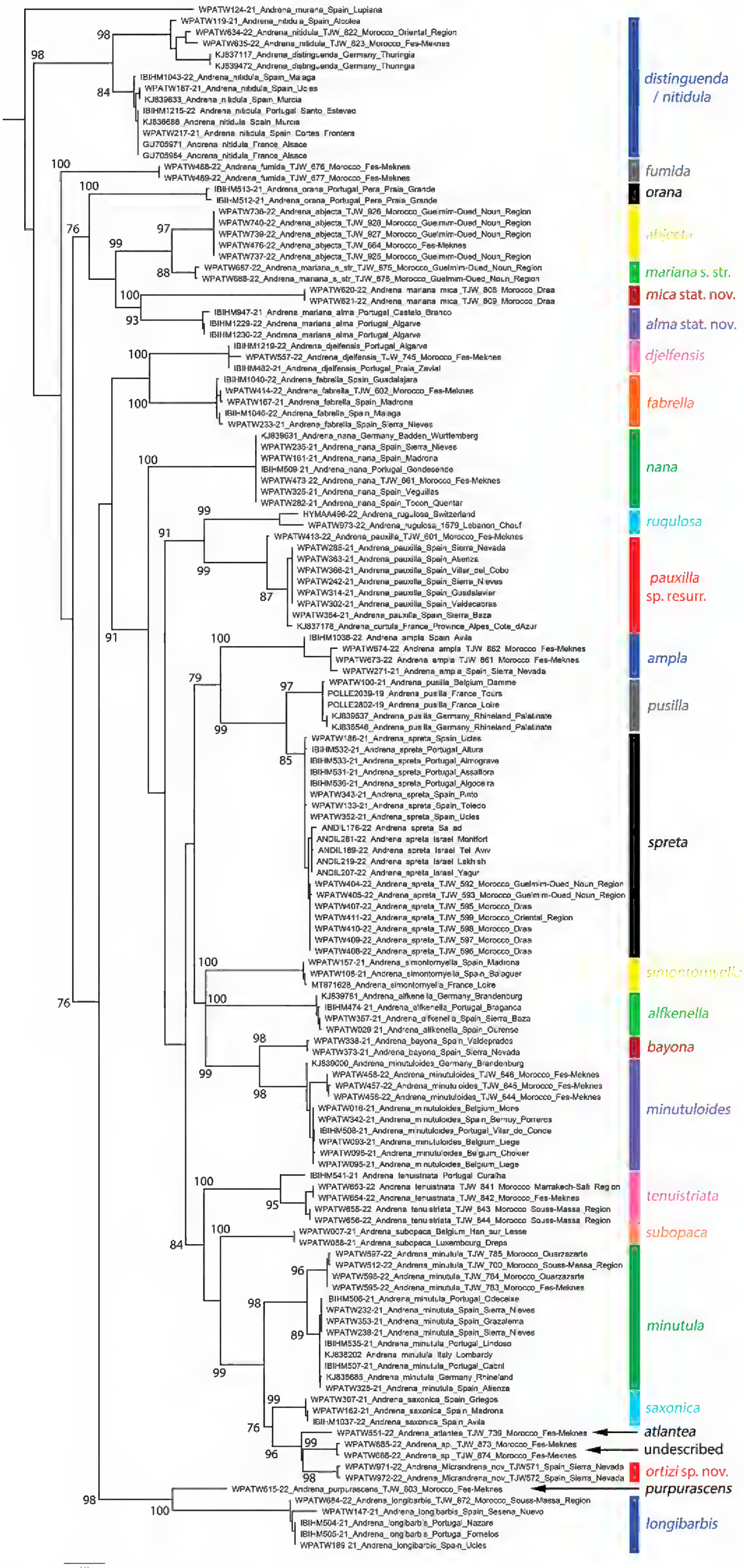

Figure 18. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Micrandrena* Ashmead, 1899 based on the mitochondrial COI gene. *Andrena* (incertae sedis) *murana* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

they are not described at this time, as it would be beneficial to have barcoded specimens to confirm this differentiation. They are therefore referred to as aff *mica* in the identification key.

It is important to note that this material does not belong to *A. abjecta*, the status of which in Iberia is unclear. Warncke (1976) did not record this species from Iberia, and only his distribution maps (Gusenleitner and Schwarz 2002) indicate the presence of this species in northern and eastern Spain. This distribution does not make sense given that all other known records of *A. abjecta* come from north-western Africa (Morocco, Algeria, Tunisia), so the species would naturally be expected to occur in southern Iberia. Dardón (2014) listed two female specimens from Huelva (22.iv.1987) and Zaragoza (9.iii.1991). The specimen from Huelva may represent the undescribed aff *mica* taxon, but it is more difficult to conclude on the specimen from Zaragoza. For now, *A. abjecta* is retained on the Iberian list, but I have not examined any specimens and I consider its presence in Iberia doubtful.

Material examined. ***Andrena alma*:** **Portugal:** Albandeira, near Lagoa, 20.iv.2005, 1♀, leg. D.W. Baldock, TJWC; Algarve, Casaqueimada (7 km N of Silves), 20.iii.1995, 1♀, leg. T. & M. Simon Thomas, RMNH; Algarve, Monte Gordo, Retur, Praia do Cabeço, 29.iii.2022, 1♂, leg. T.J. Wood, TJWC; Algarve, Tavira, Cacela Velha, 28.iii.2022, 1♂, leg. T.J. Wood, TJWC; Castelo Branco, Fundão Vale de Prazeres, 17.iv.2021, 1♀, leg. C. Siopa, FLOW; **Spain:** El Soldado, Córdoba [38.3747°N, -5.0001°E], 1♀, leg. Seyrig, OÖLM (holotype); Almodóvar del Campo (Ciudad Real), 700 m, 24.iii.2005, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Santa Ana la Real, Sierra Aracena (Huelva), 630 m, 13.iv.2006, 2♂, leg. F.J. Ortiz-Sánchez, FJOS; El Hongo (P.N. Doñana), 30.iii.2018, 1♂, leg. F. Molina, EBDC.

***Andrena mariana* s. str.:** **Algeria:** Saida, 15 km S of Sfissifa, Ben Ikhou, st. 6, 6.iv.1983, 6♀, leg. R. Leys & P. v. d. Hurk, RMNH; 23 km NE of Ras El Ma, st. 38, 26.iv.1983, 1♀, leg. R. Leys & P. v. d. Hurk, RMNH; Dayet el Kerch [Daïet el Kerch], st. 5, 5.iv.1983, 2♀, leg. R. Leys & P. v. d. Hurk, RMNH; **Morocco:** Guelmim-Oued Noun, Guelmim, Asrir, 1 km W, 20.iii.2022, 1♀, leg. T.J. Wood, TJWC; **Spain:** Fuerteventura, Valley Granadillos [28.3864°N, -14.0865°W], 17.iv.1934, 1♀, OÖLM (holotype); **Tunisia:** Ksar Hadada, 4–5.iv.1996, 46♀, leg. K. Deneš, OÖLM; M'saken, 20–21.iv.1998, 2♀, leg. K. Deneš, OÖLM; Wadi Ram, 45 km E Douz, 4.iv.2006, 1♀, leg. J. Straka, OÖLM.

***Andrena mica*:** **Algeria:** Ghardaia [32.5047°N, 3.6419°E], 1♀, OÖLM (holotype); **Morocco:** 30 km E Midelt, 13.v.1995, 1♀, leg. Mi. Halada, OÖLM; Drâa-Tafilalet, Ouarzazate, P1506, Telouet, Adaha, 1700 m, 18.iv.2022, 6♀, leg. T.J. Wood, TJWC; Drâa-Tafilalet, Ouarzazate, 2 km W Agouim, 1800 m, 13.iv.2022, 3♀, leg. T.J. Wood, TJWC; Ifkern, 25 km E Boulemane, 24.v.1995, 1♀, leg. Mi. Halada, OÖLM; M'rirt (30 km N), 11.iii.1989, 1♀, leg. H. Teunissen, RMNH; **Tunisia:** Hammamet env, 15.iii.1996, 1♀, leg. K. Deneš, OÖLM; Kasserine, 13.iv.1998, 1♀, leg. K. Deneš, OÖLM; Nefta [Naftah], 20.v.1993, 1♀, leg. J. Batelka, OÖLM.

***Andrena* aff *mica*:** **Spain:** 40 km W Málaga, Yunquera, 800 m, 29.iv.2003, 5♀, leg. J. Halada, OÖLM/TJWC; La Corchuela (Dos Hermanas, Sevilla), 35 m,

27.iii.2009, 2♂, 2♀, leg. F.J. Ortiz-Sánchez, FJOS; Río Blanco, Aguadulce (Sevilla), 300 m, 17.v.2008, 1♀, leg. F.J. Ortiz-Sánchez, FJOS.

***Andrena nitidula*: Algeria:** Babor, 1♀, MNHN (false lectotype of *A. obsoleta*).

***Andrena obsoleta*: Algeria:** Bône [=Annaba, 36.9092°N, 7.7264°E], 1♀, MNHN (lectotype of *A. obsoleta*, by present designation); 23 km NE of Ras El Ma, st. 38, 26.iv.1983, 1♀, leg. R. Leys & P. v.d. Hurk, TJWC; 5 km N of Mecheria, Djebel Antar, st. 10, 7.iv.1983, 1♀, leg. R. Leys & P. v.d. Hurk, RMNH; **Italy:** Sicilia orient., Taormina, 200 m, Ghardino [Giardini Naxos], 25.iii.1950, 1♂, Hartig & Grisham, MZUR; **Tunisia:** Tunis, 1911, 3♀, leg. O. Schmiedeknecht, SMFD.

***Andrena tenostra*: Spain:** Villajoyosa [38.5097°N, -0.2299°E], 11.v.1936, 1♀, leg. Andréu, OÖLM (holotype); Salobreña, Granada, 8.v.1983, 3♀, leg. W. Perrandin, OÖLM/TJWC.

Andrena (*Micrandrena*) *distinguenda* Schenck, 1871 and *Andrena* (*Micrandrena*) *nitidula* Pérez, 1903

The status of these two species has been extensively argued over, and despite much attention the position remains somewhat unclear. Warncke (1967) argued that *A. distinguenda* Schenck, 1871 was an unavailable name because it was preoccupied by *A. distinguenda* Schenck, 1853. He then authored the replacement name *A. obsoleta spongiosa* Warncke, 1967, using the incorrect concept that *A. obsoleta* was the oldest available name for this group of species, as discussed above. Schönitzer et al. (1992) clarified the situation, and argued that *A. distinguenda* Schenck, 1853 was a *nomen nudum* because it appears without a description in a discussion concerning species related to *A. bicolor*. As a *nomen nudum*, the name is available and cannot preoccupy its later usage. Therefore, the name *A. distinguenda* Schenck, 1871 is both available and valid as the senior synonym; *A. obsoleta spongiosa* is consequently an unnecessary replacement name.

Andrena distinguenda was described from western Germany, and *A. nitidula* was described from south-western France (lectotype from Bordeaux [though this is not indicated on the specimen, it bears the number '675' which refers to the entry for *A. nitidula* in the catalogue of Pérez], designated by Warncke 1967, Fig. 19). As discussed above, Warncke (1967) incorrectly recognised a specimen that morphologically corresponds to *A. nitidula* as the lectotype of *A. obsoleta*, and then synonymised *A. nitidula* with *A. obsoleta*. He then treated *A. distinguenda* Schenck, 1871 as a subspecies of *A. obsoleta* in the form *A. obsoleta spongiosa*. He then later adopted a three subspecies model, *A. o. obsoleta* (North Africa), *A. o. nitidula* (Western Europe), and *A. o. spongiosa* (Central Europe) (see Schönitzer et al. 1992), finally introducing a fourth subspecies *A. o. puella* Alfken, 1938 in Sardinia and Sicily (see Gusenleitner and Schwarz 2002). Schönitzer et al. (1992) argue that both *A. distinguenda* and *A. nitidula* can be morphologically separated in north-western Italy (Bordighera). They argue that *A. nitidula* occurs in North Africa, citing Pérez (1903) and Alfken (1914). They also argue that specimens from southern Spain (Tarifa) appear to be somewhat intermedi-

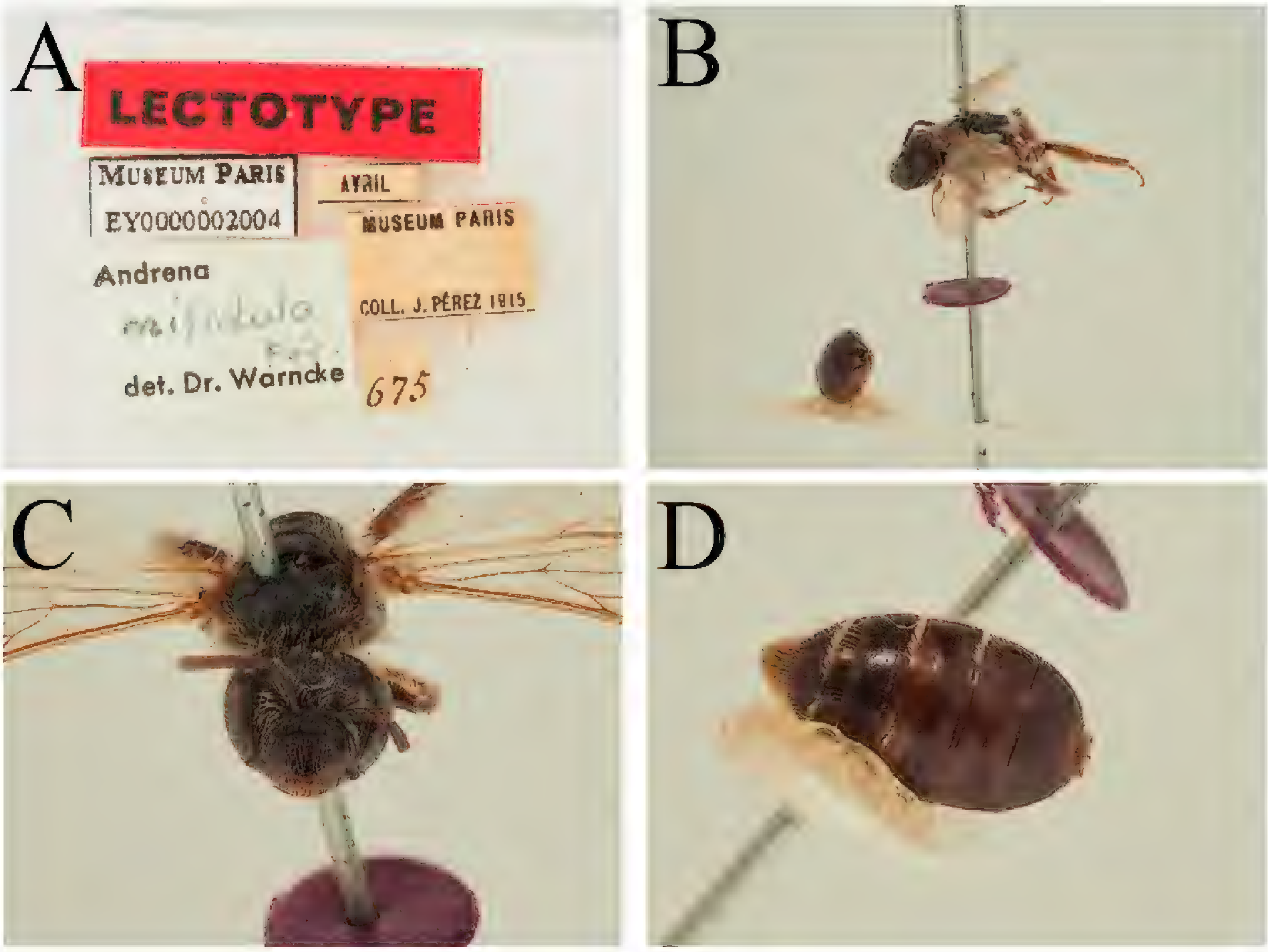

Figure 19. *Andrena* (*Micrandrena*) *nitidula* Pérez, 1903, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

ate between *A. distinguenda* and *A. nitidula*, concluding that the question as to whether there are two species or simply a very variable single species remains open.

Burger and Herrmann (2003) revised European material from this species pair using the names *A. distinguenda* and *A. nitidula*, after having examined syntypes of *A. nitidula* in the ZMHB collection. Using morphological characters, they conclude that (in a European context) *A. distinguenda* has a predominantly eastern distribution, from Central Europe to Greece, with populations also in the south of France and a few records from north-eastern Spain. In contrast, *A. nitidula* is a western species, from Iberia to the south and east of France and into south-western Germany and the north-west of Italy. They reach the same conclusion as Schönitzer et al. (1992), that where these two forms occur in sympatry (Germany, France, Italy) they can be morphologically separated. They do not conclude on the status of *A. obsoleta*, but note that *A. nitidula* occurs in North Africa, and that Warncke's treatment is unclear. This problem arises because it does not appear that any of the authors of Schönitzer et al. (1992) or Burger and Herrmann (2003) inspected the lectotype of *A. obsoleta* designated by Warncke in the MNHN. This lectotype bears a handwritten label that the lectotype designation is incorrect, and that the specimen corresponds to *A. distinguenda* Schenck (Fig. 16A). However, it is unclear who wrote this, as neither Schönitzer et al. (1992)

nor Burger and Herrmann (2003) mention this explicitly, and I do not recognise the handwriting on the label.

Barcode analysis complicates this matter further (Fig. 18). Analysis of sequences from France, Germany, Morocco, Portugal, and Spain shows the presence of two clear clades. One clade is composed of specimens identified as *A. nitidula* from France, Portugal, and Spain, including specimens from the south of Iberia (Algarve, Málaga, Murcia). This clade would appear to be the true *A. nitidula*. However, the second clade contained sequences from specimens identified as *A. distinguenda* from central Germany, but also from a specimen identified as *A. nitidula* from central Spain (Guadalajara) and two specimens identified as *A. nitidula* from northern Morocco (Fès-Meknes, Oriental). These two clades were consistently separated genetically, by an average genetic distance of 7.08% (range 5.58–8.77%). The nominally true *A. nitidula* clade showed low intraspecific variation of 0.26% (range 0.00–0.63%). However, the situation in the clade containing *A. distinguenda* sequences from Germany showed intraspecific variation of 2.84% (range 0.00–4.10%), with the 4.10% genetic distance recorded between specimens from Germany and the Middle Atlas (Bakrit, near Azrou) in Morocco.

Morphologically, both Spanish and Moroccan specimens falling into the *A. distinguenda* clade conform to the concept of *A. nitidula* using the criteria specified by Burger and Herrmann (2003). Indeed, all material I have identified from north-western Africa morphologically conforms to the concept of *A. nitidula* sensu Burger and Herrmann. Although the genetic data strongly supports the existence of two species, the conflict between the genetic and morphological results suggests that, at the moment, they cannot be consistently separated morphologically across their range. No taxonomic action is taken here, and the morphological criteria of Burger and Herrmann (2003) are followed for the purpose of the identification key. In Iberia, *A. nitidula* is considered to be present throughout, but *A. distinguenda* is limited to the extreme north-east of Spain. However, it is clear that there is a major disagreement between the morphological and genetic methods, and these two species may ultimately not be consistently separable. Further analysis using more powerful genetic techniques is necessary.

Relictual species morphologically related to *Andrena* (*Micrandrena*) *rugulosa* Stöckhert, 1935

Inspection of *Micrandrena* specimens from high altitude in the Sierra Nevada revealed the presence of a species that morphologically resembles *A.* (*Micrandrena*) *rugulosa* Stöckhert, 1935 due to its head that is only slightly shorter than wide rather than clearly shorter than wide, an unusual character in *Micrandrena*. This finding is remarkable, because although widely distributed in Central and Eastern Europe, *A. rugulosa* has a western limit in the Swiss Alps, and has not been previously recorded from France, Spain, or Portugal (Gusenleitner and Schwarz 2002). Samples collected from the Sierra Nevada at high altitude (2000–2100 m) during 2021 are strongly differentiated from *A. rugulosa*, separated by an average genetic distance of 16.01% (range 15.81–16.41%;

Fig. 18). Instead, they form a clade with bootstrap support of 96 with sequences of *A.* (*Micrandrena*) *atlantea* Wood, 2021 (High and Middle Atlas in Morocco) and a morphologically similar undescribed *Micrandrena* from high altitude (1800–1900 m) in the Moroccan Middle Atlas.

The Sierra Nevada sequences were separated from *A. atlantea* by an average genetic distance of 6.04% (range 5.71–6.38%) and from the undescribed *Micrandrena* by an average genetic distance of 6.34% (range 6.31–6.38%). These three species would therefore seem to represent an isolated *Micrandrena* lineage that is restricted to the Sierra Nevada and the High and Middle Atlas Mountains in Morocco, with consequent genetic and morphological divergence. This is the same pattern as observed in the subgenus *Euandrena*, suggesting that the Sierra Nevada hosts the remnants of a fauna that was presumably once more widespread across Iberia and North Africa. Additional sampling and genetic analysis is required to determine if this pattern holds true for other bee groups. The new *Micrandrena* species from the Sierra Nevada is described below, and the undescribed *Micrandrena* species from Morocco will be described in an upcoming publication.

***Andrena* (*Micrandrena*) *niveata* Friese, 1887 sensu lato**

Andrena niveata was described from Germany and Hungary, without further information (Friese 1887). The exact type locality is unclear, as well as the type depository, with no clearly identifiable syntypes located during searches in the SMFD and ZMHB collections, the suggested possible depositories (Gusenleitner and Schwarz 2002). Nevertheless, the concept of *A. niveata* in Central Europe is clear, and *A. niveata* is a well-defined species in this region (Schmid-Egger and Scheuchl 1997; Gusenleitner and Schwarz 2002; Amiet et al. 2010). Warncke described three subspecies; *A. n. lecana* Warncke, 1975 (Spain; *locus typicus*: Rivas-Vaciamadrid), *A. n. haloga* Warncke, 1980 (Italy; *locus typicus*: Lecce), and *A. n. bubulca* Warncke, 1975 (Turkey; *locus typicus*: Erzurum); the status of the Italian and Turkish subspecies is not addressed here. Unfortunately, all nine freshly collected *A. n. lecana* specimens from central and southern Spain (including from the *locus typicus*) sent for genetic analysis failed to produce sequences. More specific primers will be required to address this question using genetic evidence.

Warncke (1975a) described *A. n. lecana* extremely briefly, noting that in both sexes the first tergum was finely but clearly shagreened, and finely but more strongly punctured than in *A. niveata* s. str., with the following terga also more clearly and strongly punctured. He then gave a distribution of *A. n. lecana* across much of central Spain south to hilly parts of the provinces of Granada (Huéscar) and Almería (Tíjola). In contrast he gives a distribution for *A. niveata* s. str. of the whole of Iberia, though his distribution maps (Gusenleitner and Schwarz 2002) show a distribution covering eastern, central, and south-eastern Spain. There is therefore the possibility that the two subspecies exist in sympatry, suggesting that they may be distinct.

Examination of material from Spain shows that the two taxa are distinct, but morphological separation is challenging, may not be possible in all cases when old,

abraded, or dirty specimens are available, and is best made with reference to the male genital capsule. Taking male specimens, the shape of the gonostyli are distinctive. In *A. niveata* s. str., the gonostyli are elongate, with the inner margins of the gonostyli only weakly produced towards the penis valves (Fig. 20A). In contrast, in *A. n. lecana*, the inner margins of the gonostyli are strongly and clearly produced towards the penis valves (Fig. 20B); the apical spatulate part of the gonostyli are also comparatively shorter, thus the gonostyli appear shorter and more compact in *A. n. lecana* and longer and more elongate in *A. niveata* s. str. The structure of the genital capsule of *A. niveata* s. str. is consistent across Spain to the province of Málaga (the most southerly *A. niveata* s. str. male examined). Furthermore, the male scutum is shagreened in *A. niveata* s. str., whereas it is extensively shiny in *A. n. lecana*, and the terga are also more strongly shagreened in *A. niveata* s. str. compared to *A. n. lecana* (Fig. 20C, D). Separation of females (recognised by their wide and poorly defined propodeal triangle, Fig. 20E, F, in combination with their depressed tergal margins) is more challenging and may not be possible in all situations. Typically, *A. niveata* s. str. has the terga shagreened, with punctures on the tergal discs partially disappearing into this shagreenation (Fig. 20G). In contrast, *A. n. lecana* has the terga shiny, almost without shagreen, with the dense punctures on the tergal discs strong and clearly visible, not disappearing due to the absence of background shagreenation (Fig. 20H). The scutum and scutellum are also more extensively shiny, whereas in *A. niveata* s. str. these areas usually show at least some shagreenation and are never polished and smooth. The problem comes that some individuals nominally assigned to *A. niveata* s. str. have partially shing terga, and without genetic sequences it is not possible to say with complete confidence if they belong to *A. niveata* s. str. or *A. n. lecana*. Moreover, all Iberian *A. niveata* s. str. have tergal shagreenation that is weaker than that of *A. niveata* s. str. populations in Central Europe.

The position is taken here that the strength of tergal shagreenation in *A. niveata* s. str. females is variable across Europe, but that *A. lecana* stat. nov. is a valid species based on the overlapping range in combination with the consistent difference in the shape of the male genital capsule. It has a distribution across steppic parts of central Spain, extending into mountainous areas in south-eastern Spain. Females displaying any level of shagreenation on the tergal discs are considered to represent Iberian populations of *A. niveata* s. str., and females with completely polished tergal discs without a trace of shagreenation represent *A. lecana* (see identification key). Future genetic investigation using more targeted primers will be necessary to confirm this position. Finally, specimens of *A. lecana* from high altitude in the Sierra Nevada show slightly different antennal ratios in the male sex, though the male genital capsule is otherwise identical; this requires further investigation.

Material examined. ***Andrena lecana*: Spain:** Ribas [Rivas-Vaciamadrid, 40.3503°N, -3.5390°E], 6.v.1908, 1♀, leg. Dusmet, OÖLM (holotype); Carboneras de Guadazaón (Cuenca), 1030 m, 16.v.2009, 1♀, leg. F.J. Ortiz-Sánchez, FJOS; Guadalajara, Alcolea del Pinar, 12.v.2021, 1♀, leg. T.J. Wood, TJWC; Guadalajara, Lupiana, 12.v.2021, 1♀, leg. T.J. Wood, TJWC; Huéscar (Granada), 1900, 1♂, leg. Escalera, OÖLM (paratype); La Cabrilla, Sierra Cazorla (Jaén), 1600 m, 1–3.vi.2022,

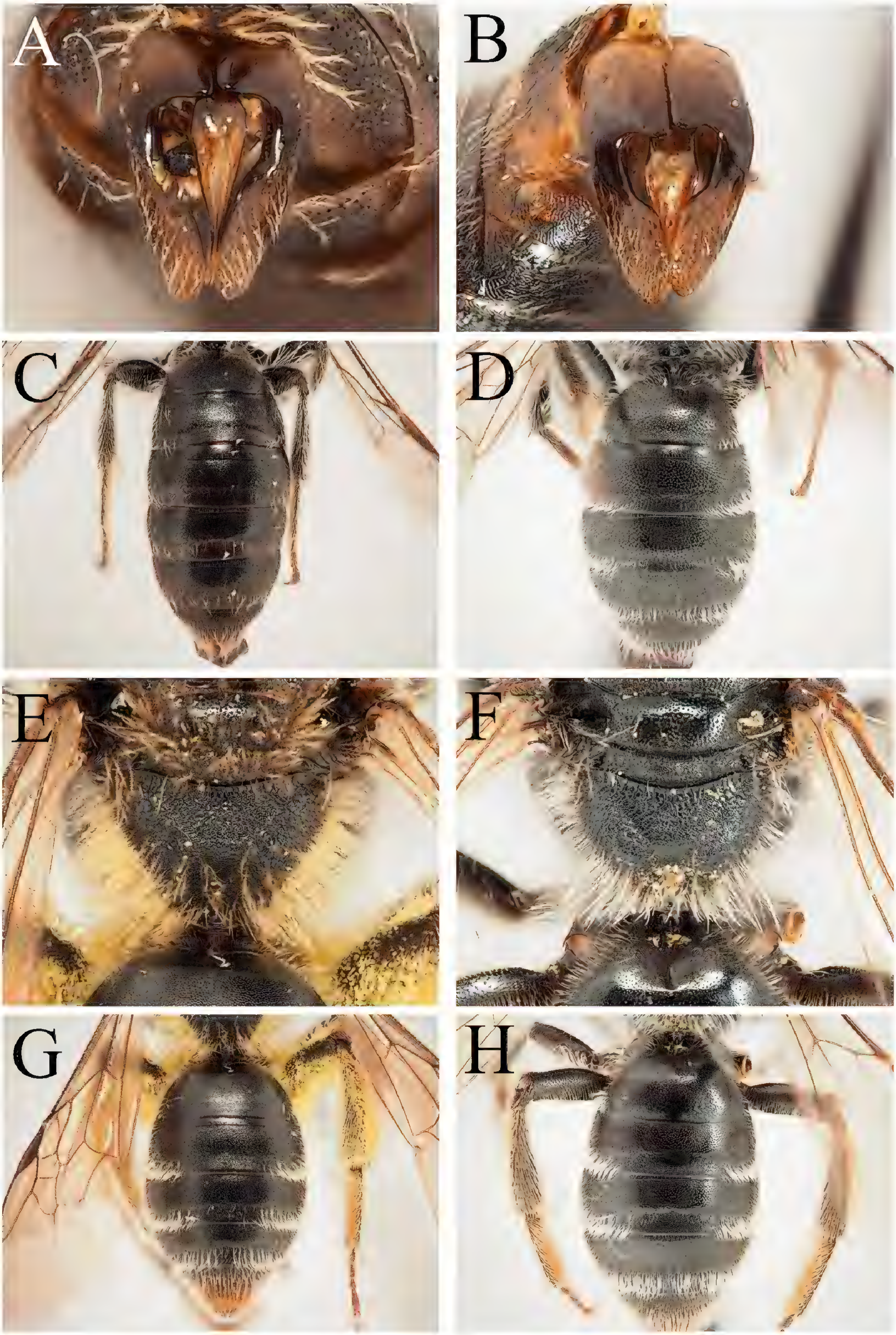

Figure 20. *Andrena* (*Micrandrena*) *niveata* Friese, 1887 **A** male genital capsule **C** male terga, dorsal view **E** female propodeal triangle **G** female terga, dorsal view; *Andrena* (*Micrandrena*) *lecana* Warncke, 1975 **B** male genital capsule **D** male terga, dorsal view **F** female propodeal triangle **H** female terga, dorsal view.

1♀, leg. C.M. Hererra, CMHC; Madrid, Rivas-Vaciamadrid, Canal de Manzanares to Camino de Uclés, 19.v.2021, 2♀, leg. T.J. Wood, TJWC; Órgiva, N, 1300 m, Sierra Nevada, 26.vi.1988, 1♀, leg. M. Schwarz, OÖLM; Pozuelo, La Fuente, 1♂, OÖLM (paratype); Segovia, Madrona, 500 m NE, Arroyo del Hocino, 15.v.2021, 2♀, leg. T.J. Wood, TJWC; Sierra Nevada, Trevélez, Refugio La Campiñuela, 2400 m, 14.vi.2021, 7♂, 2♀, leg. T.J. Wood, TJWC.

***Andrena niveata* s. str.: Spain:** Cáceres, Cuacos de Yuste, 500 m, 11.v.1999, 1♀, leg. H. & J.E. Wiering, RMNH; Cádiz, Grazalema, Río Guadalete, 28.v.2021, 1♀, leg. T.J. Wood, TJWC; Cádiz, Embalse de Barbate Sw, 1♂, 3♀, 6.v.2017, leg. Barták & Kubik, OÖLM/TJWC; Granada, Sierra de Baza, Prados del Rey, 2000 m, 19.vi.2021, 11♀, leg. T.J. Wood, TJWC; Málaga, 5 km W of Alhaurín de la Torre, 4.vi.1962, 1♀, leg. Jeekel & Wiering, RMNH; Málaga, Cortes de la Frontera, path to Llano de las Labores, 26.v.2021, 3♀, leg. T.J. Wood, TJWC; Málaga, Estepona, 21.iv.1983, 1♀, leg. H. Teunissen, RMNH; Navarra, Tudela, 16.iv.1978, 1♀, leg. C. Gielis, RMNH; Gerona, Figueras, 15.iv.1971, 1♀, leg. J. Leclercq, UMONS.

Andrena (*Micrandrena*) *spreta* Pérez, 1895, *Andrena* (*Micrandrena*) *curtula* Pérez, 1903, *Andrena* (*Micrandrena*) *pusilla* Pérez, 1903, and *Andrena* (*Micrandrena*) *pauxilla* Stöckhert, 1935

Members of this species group are challenging to identify and have been inconsistently treated in the literature, with variable species concepts. *Andrena spreta* was described from Algeria, with Warncke (1967) designating a lectotype from Biskra (Fig. 21A; Pérez also mentions a female from Constantine in his catalogue). *Andrena curtula* was described from north-eastern Spain, with Warncke (1967) designating a lectotype from Barcelona (Fig. 21B). *Andrena pusilla* was described from the south of France (Bordeaux, Nantes) and Spain, with Warncke (1967) designating a lectotype from Nantes (Fig. 21C). Finally, *A. pauxilla* was described from the Upper Rhine valley in south-western Germany, with Stöckhert (1935) designating a female from Karlsruhe as the holotype.

Warncke (1967) recognised three species, *A. spreta*, *A. curtula*, and *A. pauxilla*, treating *A. pusilla* as a subspecies of *A. spreta*. Warncke (1974) recognised only one taxon in North Africa (*A. spreta spreta*), but Warncke (1976) surprisingly recognised only *A. spreta pauxilla* in Iberia, not mentioning *A. curtula* as a species despite its description from Iberia, only referring to its listing in Ceballos (1956) but indicating that this referred to *A.* (*Micrandrena*) *tenuistriata* Pérez, 1895. This treatment is difficult to understand. Warncke later adopted an extremely broad position (see distribution maps in Gusenleitner and Schwarz 2002), lumping all members of the group into a broad *A. spreta*. In this model, *A. spreta* s. str. was restricted to North Africa, *A. spreta curtula* was distributed across Iberia to southern France, *A. spreta pusilla* was found in northern and Central Europe, with two more subspecies in i) Italy and ii) south-eastern Europe to the Levant.

This position was not adopted by subsequent authors. Schwarz et al. (1996) accepted *A. pusilla* as a valid species, as well as *A. curtula*. However, they synonymised *A. pauxilla* with *A. curtula*. Schmid-Egger and Scheuchl (1997) did not follow this inter-

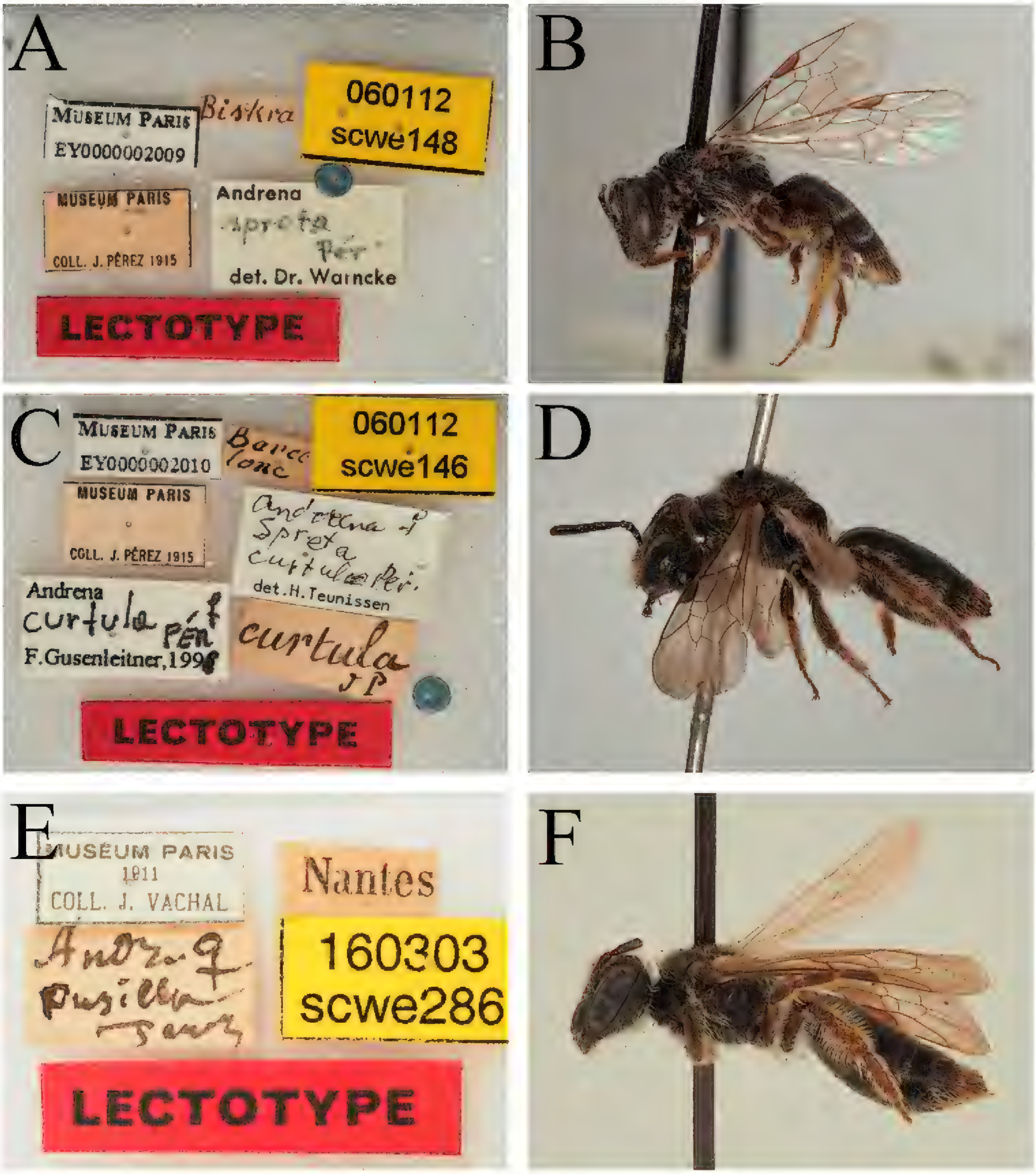

Figure 21. *Andrena* (*Micrandrena*) *spreta* Pérez, 1895, female lectotype **A** label details **B** profile; *Andrena* (*Micrandrena*) *curtula* Pérez, 1903, female lectotype **C** label details **D** profile; *Andrena* (*Micrandrena*) *pusilla* Pérez, 1903, female lectotype **E** label details **F** profile.

pretation, treating *A. pauxilla* as a distinct species, though Amiet et al. (2010) followed the position of Schwarz et al. (1996). Dardón (2010) and Dardón et al. (2014) accepted only a broad *A. spreta* taxon, including *A. curtula*, *A. pusilla*, and *A. pauxilla*, recognising *A. spreta* s. str. and *A. spreta pusilla* in an Iberian context. The situation is therefore unclear, both for the number of species present in this complex, and their distributions.

Analysis of barcodes provides unambiguous support for the existence of three distinct species (Fig. 18), *A. spreta* including *A. curtula*, *A. pusilla*, and *A. pauxilla* sp.

resurr. Specimens of *A. spreta* from Israel, Morocco, Portugal, Spain formed a clear clade with bootstrap support of 85. These sequences were separated by an average genetic distance of 0.45% (range 0.00–1.07%). They were clearly separated from a sister clade of *A. pusilla* sequences from Belgium, France, and Germany by an average genetic distance of 4.33% (range 3.88–4.84%). The *A. pusilla* clade had low intraspecific genetic distance of 0.29% (range 0.00–0.71%). *Andrena pauxilla* was strongly differentiated and was found as sister to *A.* (*Micrandrena*) *rugulosa*, showing average genetic differentiation of 10.96% (range 10.38–11.85%) from *A. spreta* and 11.69% (range 10.75–12.59%) from *A. pusilla*. This *A. pauxilla* clade includes a specimen from the south of France (KJ837178, Lac St. Croix) that was identified as *A. curtula*, the genetic results suggest that it is misidentified. Morphologically, *A. pauxilla* is clearly differentiated from *A. spreta* and *A. pusilla* due to the absence of a gradulus at the base of the terga. Confusion is impossible in the female sex after recognition of this character; the foveae are also longer and narrower and filled with white rather than light brown hairs, the scutum is more densely and uniformly punctate when compared to *A. spreta*. Examination of the lectotypes of *A. spreta* and *A. curtula* shows no clear structural difference. The degree of shagreenation varies, but this is typical for *A. spreta* across its range; both lectotype specimens show the presence of a gradulus at the base of the terga, excluding their conspecificity with *A. pauxilla*. Due to these genetic results combined with the morphology of the lectotype specimens, the synonymy of *A. curtula* with *A. spreta* as proposed by Dardón (2010) and Dardón et al. (2014) is therefore followed, though their synonymies of *A. pusilla* and *A. pauxilla* with *A. spreta* are rejected.

A single barcode was available from Moroccan specimens from the Middle Atlas tentatively identified as *A. pauxilla* which showed an average genetic distance to European *A. pauxilla* specimens of 2.00% (range 1.48%–2.29%). This is considered to represent only separation by distance, and thus *A. pauxilla* is recorded for the first time in North Africa and unambiguously recorded in Spain. Within Spain, *A. pauxilla* appears to be principally recorded from mountain ranges such as the Sierra de las Nieves, the Sierra Nevada (Fig. 22A, B), Sierra Cazorla, Sistema Central, and Sistema Ibérico (Fig. 22C, D). *Andrena pauxilla* would therefore have a currently known distribution of Morocco, Spain, France, and Germany. On the basis of these results, *A. spreta* would appear to be a pan-Mediterranean species, and *A. pusilla* its predominantly northern counterpart (though the species descends south into Italy). The two species can be found in sympatry in the south of France (Praz, in litt.), but to date I have examined no *A. pusilla* specimens from Iberia. Due to the confusion in this group, it must be considered absent until it can be positively demonstrated to be present south of the Pyrenees.

Material examined. ***Andrena curtula*: Spain:** Barcelona [41.4028°N, 2.1332°E], 1♀, MNHN (lectotype; Fig. 21B).

***Andrena pauxilla*: France:** Bischenberg, 28.vi.1936, 1♀, leg. M. Klein, det. E. Stöckhert, OÖLM; Hausbergen, 29.vi.1930, 1♀, leg. M. Klein, det. H.R. Schwenninger, OÖLM; **Morocco:** Fès-Meknès, Boulemane, R503, 7 km SE of Boulemane, 1900 m, 22.v.2022, 1♂, 1♀, leg. T.J. Wood, TJWC; **Spain:** Canet de Mar, 26.iii.1963, 1♀, leg. F. Vergés, det. H.R. Schwenninger, OÖLM; Cuenca, Huerta del

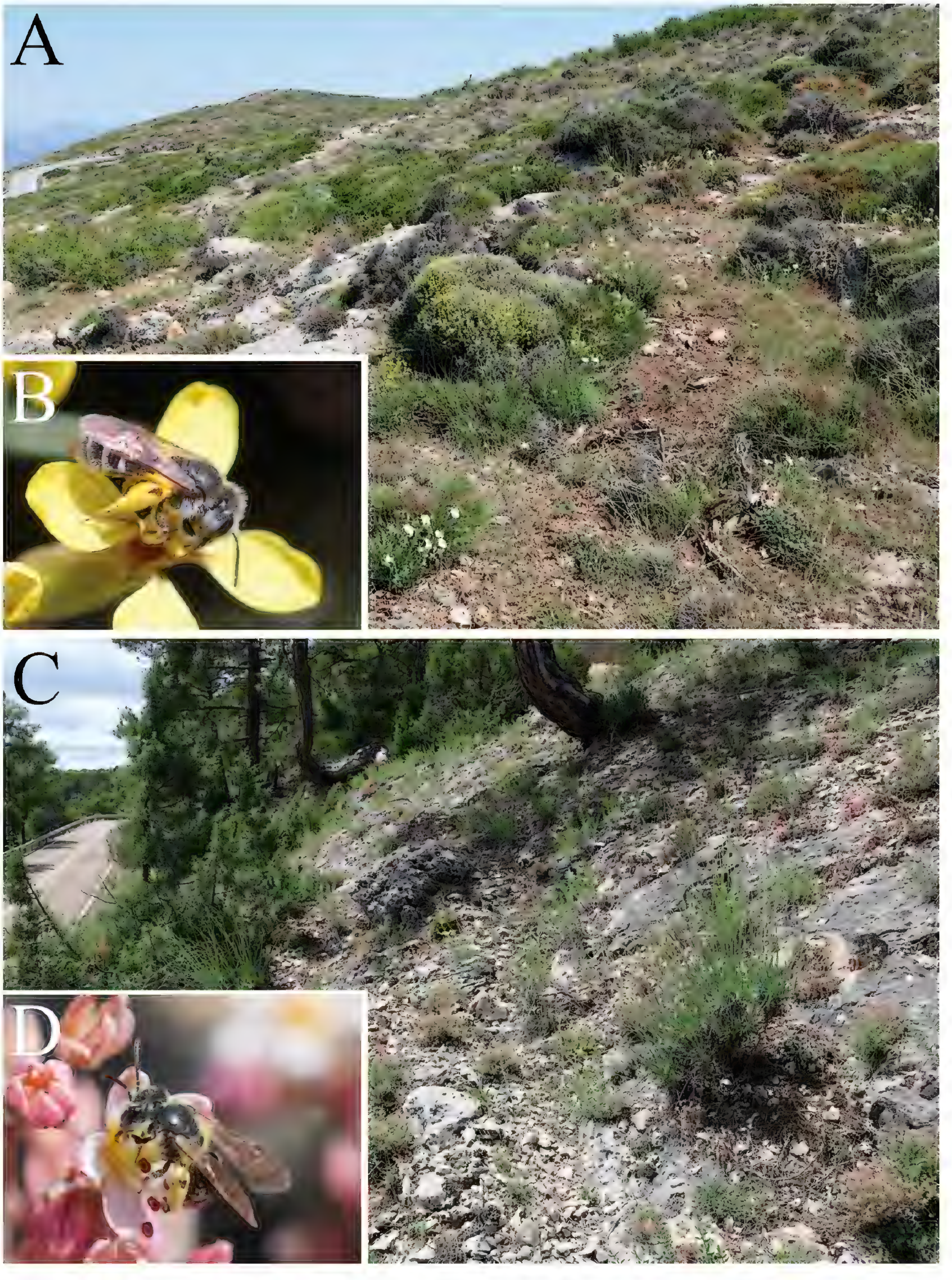

Figure 22. *Andrena* (*Micrandrena*) *pauxilla* Stöckhert, 1935 **A** habitat, Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 2100 m, 12.vi.2021 **B** female collecting pollen from *Vella spinosa* (Brassicaceae) **C** habitat, Cuenca, Mirador Valle de Valdecabras, 21.vi.2021 **D** female collecting pollen from *Sedum* spp. (Crassulaceae).

Marquesado, environs north of town, 26.vi.2021, 3♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Jardín Botánico Hoya de Pedraza environs, 1900 m, 9.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Mirador Monte Ahí de Cara,

2100 m, 12.vi.2021, 1♀, leg. T.J. Wood, TJWC; Guadalajara, Aldeanueva de Atienza, 9.vii.2021, 1♀, leg. T.J. Wood, TJWC; Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 30.v.2021, 1♀, leg. T.J. Wood, TJWC; La Cabrilla, Sierra Cazorla (Jaén), 1600 m, 3.vi.2022, leg. C.M. Herrera, CMHC; Sierra Cazorla, Puerto Llano, 1800 m, 11.vi.2022, 1♂, 3♀, leg. J. Valverde, CMHC; Teruel, Guadalaviar, Rambla de los Ojos, 27.vi.2021, 1♀, leg, T.J. Wood, TJWC; Teruel, Villar del Cobo, Barranco de los Oncenachos, 27.vi.2021, 6♀, leg, T.J. Wood, TJWC; Cuenca, Mirador Valle de Valdecabras, 21.vi.2021, 2♀, leg, T.J. Wood, TJWC.

***Andrena pusilla*: France:** Nantes [47.2233°N, -1.5542°W], 1♀, MNHN (lectotype; Fig. 21C).

***Andrena spreta*: Algeria:** Biskra [34.8600°N, 5.6995°E], 1♀, MNHN (lectotype; Fig. 21A).

Andrena (*Micrandrena*) *strohmella* Stöckhert, 1928 and *Andrena* (*Micrandrena*) *icterina* Warncke, 1974

Andrena strohmella was described from southern Germany and is a typically early spring species in the Central European *Andrena* fauna, with records extending south to the High and Maritime Alps in France, and west to the Bordeaux region; it has not previously been reported from the Pyrenees (Gusenleitner and Schwarz 2002). Warncke (1974) later described *A. icterina* from northern Algeria. He later indicated the presence of this species in south-eastern Spain in his distribution maps (Gusenleitner and Schwarz 2002), though he did not list its present in Iberia (Warncke 1976). Wood et al. (2020b) later reported the presence of this species in northern Morocco. In his description of *A. icterina*, Warncke draws comparison with *A. strohmella*, noting that the process of the labrum is half as broad, the clypeus is more sparsely punctate and lacking an unpunctured midline, that the terga are more strongly shagreened, and that the carinae on the dorsolateral corners of the first tergum are more weakly pronounced. Dardón (2010) and Dardón et al. (2014) did not actually examine any material of Iberian *A. icterina*, but inspection of new Iberian material has demonstrated that *A. icterina* is more widespread in Iberia than previously thought, being found from the Los Alcornocales to the Sierra de las Nieves, the Sierra Nevada, Sierra de Baza, Sierra Cazorla, and Sistema Central, and is also newly reported from northern Portugal (see below). In all of these localities it is found in mountainous areas, generally at high altitude in excess of 1000 m.

Dardón (2010) and Dardón et al. (2014) reported *A. strohmella* from north-eastern Spain, from Tarragona: Alcanar, v.2002, leg. Kadlec, OÖLM. I have not been able to locate and examine this specimen for myself in the OÖLM collection, but it is slightly problematic for ecological regions. *Andrena strohmella* is clearly a species of deciduous temperate woodland; this is reflected in its distribution across Central Europe, and in its association with flowering trees such as *Crataegus* (Rosaceae), *Prunus* (Rosaceae), and *Salix* (Salicaceae). *Andrena strohmella* has therefore not previously been reported from Mediterranean regions. The record from Alcanar does not therefore match the ecology of this species, Alcanar being a low-elevation (c. 70 m) village close

to the Mediterranean coast. However, *A. strohmella* is present in north-eastern Catalonia based on recently collected specimens (Álvarez Fidalgo, in litt.), and so the species is retained on the Spanish and Iberian lists.

More broadly, morphological differences between *A. strohmella* and *A. icterina* are slight, though they do not appear to introgress based on examined specimens. Some characters such as the strength of the carinae on the dorsolateral corners of the first tergum are not completely consistent, because some specimens in Central Europe can be found in which these are very weakly produced. Genetic data will hopefully clarify the status of *A. icterina*, but unfortunately, like *A. lecana*, this taxon appears to be challenging to barcode, as all seven Iberian specimens sent for genetic analysis failed or returned corrupted sequences.

Material examined. ***Andrena icterina*: Portugal:** Bragança, Serapicos, 16.v.2021, 1♀, leg. A. Soares, A. Soares Coll.; **Spain:** Ávila, Hoyocasero, El Pinar de Hoyocasero, 16.v.2021, 1♀, leg. T.J. Wood, TJWC; Ávila, Navalsauz, 1 km E, Alberche stream, 16.v.2021, 1♀, leg. T.J. Wood, TJWC; Cádiz prov., Vent. L. Canillas Hozgarganta-Tal b. Jimena 250 m, 14.iv.1985, 3♀, leg. W. Schacht, OÖLM; Campamento Alfaguara (Alfacar, Granada), 1420 m, 13.v.2007, 1♂, 2♀, leg. F.J. Ortiz-Sánchez, FJOS; Cortijo Tortas, Paterna del Madera (Albacete), 1310 m, 30.iv.2022, 2♂, leg. F.J. Ortiz-Sánchez, FJOS; Granada, Sierra de Baza, Prados del Rey, 2000 m, 19.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Capileira to La Cebadilla, 1500 m, 8.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada, Jardín Botánico Hoya de Pedraza environs, 1900 m, 2♀, leg. T.J. Wood, TJWC; Granada, Venta de los Alazores, 25.v.1982, 1♀, leg. R. Leys, RMNH; La Cabrilla, Sierra Cazorla (Jaén), 1600 m, 3.vi.2022, leg. C.M. Hererra, CMHC; Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 1600 m, 30.v.2021, 3♀, leg. T.J. Wood, TJWC; Sierra Cazorla, Puerto Llano, 1800 m, 11.vi.2022, 1♀, leg. J. Valverde, CMHC; Puerto Crucetillas, Riópar (Albacete), 1340 m, 30.iv.2022, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Sierra de Cazorla, Nava de las Correhuelas, 1.v.2021, 1♂, leg. C.M. Hererra, CMHC.

Subgenus *Notandrena* Pérez, 1890

The definition of this subgenus was expanded by Pisanty et al. (2022b) to include *Carandrena* Warncke, 1968 (type species *Andrena aerinifrons* Dours, 1873). It is important to note that several species formerly placed within the *Carandrena* fall elsewhere into an undescribed subgenus, but these are desert-living species, none of which are present in Iberia. In the context of this revision, *Carandrena* is treated as a strict synonym of *Notandrena*.

Andrena (incertae sedis) *urdula* Warncke, 1965 was described from Greece and is a rare and poorly understood taxon known only from a small number of specimens. It is reliably known only from Greece (type series), Spain (central Spain), and Morocco, as the distribution map presented by Gusenleitner and Schwarz (2002: 1201) actually refers to *A.* (*Notandrena*) *ungeri* Mavromoustakis 1952; the distribution map for *A. ungeri* (p. 1200) is actually the distribution map for *A. urdula*. A barcoded specimen

from south of Madrid [WPATW351-21] does not clearly fall into the *Notandrena* group (Fig. 23); its true placement is unclear because it does not have any strong characters that lead to obvious affinities with specific groups. It is best treated as incertae sedis until more genetic data are available.

Warncke described two similar taxa in the group of small metallic green *Notandrena*, *A.* (*Notandrena*) *reperta* Warncke, 1974 and *A.* (*Notandrena*) *reperta varuga* Warncke, 1975. Warncke actually described *A. reperta* as a subspecies of *A. varuga*, but due to the order of publication, *A. reperta* has priority. Both species can be recognised because the hind tibial spur is apically curved, though this character is more pronounced in Iberian specimens. Genetically, specimens of *A. reperta* from Morocco and *A. reperta varuga* from central Spain formed a clade with a specimen of *A.* (*Notandrena*) *nigroviridula* Dours, 1873 from Morocco. All three taxa were well separated; *A. reperta* and *A. reperta varuga* by 12.84%, *A. reperta* and *A. nigroviridula* by 11.67%, and

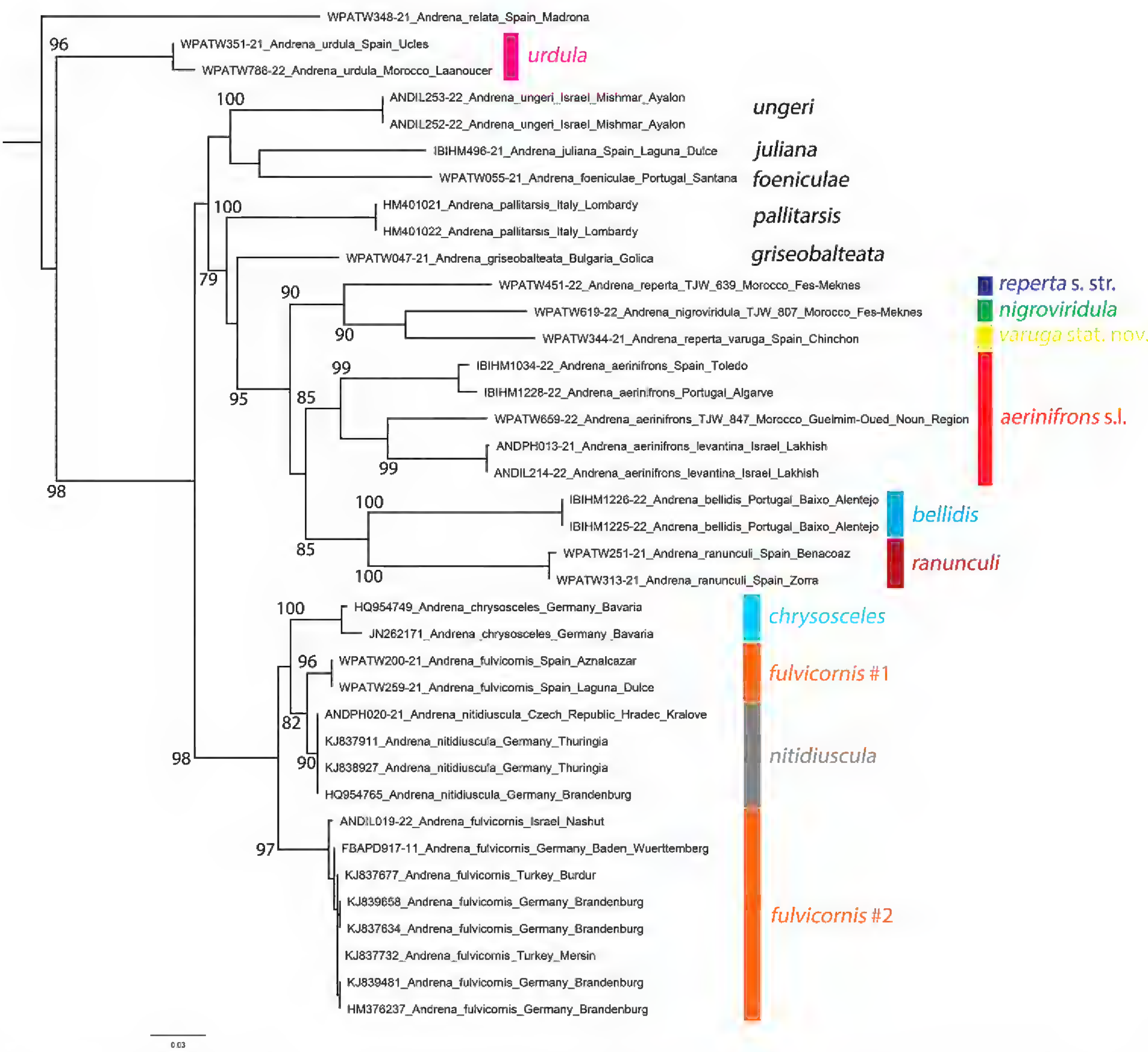

Figure 23. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Notandrena* Pérez, 1890 based on the mitochondrial COI gene. *Andrena* (incertae sedis) *relata* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

A. reperta varuga and *A. nigroviridula* by 10.12% (Fig. 23). Moreover, *A. reperta* and *A. reperta varuga* do not form a monophyletic clade, being rendered paraphyletic by *A. nigroviridula*. On this basis, *A. varuga* stat. nov. is raised to species status. *Andrena varuga* is endemic to Spain, and *A. reperta* is found in Morocco, Algeria, and Tunisia.

Dours (1873) described *A. aerinifrons* from Algeria, and *A. aerinifrons levantina* Hedicke, 1938 was later described from the Levant. Barcode analysis shows that specimens from Israel, Morocco, Portugal, and Spain show high average intraspecific variation of 8.64% (range 0.00–11.67%). The Moroccan specimen is intermediate between the Iberian and Levantine sequences, being separated from the Iberian sequences by an average genetic distance of 9.92% (range 9.73–10.12%) and from the Levantine sequences by 10.12% (range 10.12–10.12%). Given that these sequences form a monophyletic clade, a broad interpretation of *A. aerinifrons* is taken here; a neotype can be designated for *A. aerinifrons* at a later date when the situation becomes clearer, as Dours' collection was destroyed in a fire and is not available for study (see below).

Andrena (*Notandrena*) *fulvicornis* Schenck, 1861 has been recognised as distinct from *A.* (*Notandrena*) *nitidiuscula* Schenck, 1853 (Schmid-Egger and Doczkal 1995; Schmid-Egger and Scheuchl 1997; Schwenninger 2013; Bénon and Praz 2016). Barcode analysis shows that specimens from Germany, Israel, and Turkey are indeed clearly distinct from *A. nitidiuscula*, not forming a sister clade and showing average separation of 3.79% (range 3.50–3.89%), with bootstrap support of 96. However, sequences of putative *A. fulvicornis* from Spain fall into a clade of *A. nitidiuscula* and *A.* (*Notandrena*) *chrysosceles* (Kirby, 1802). Spanish specimens are separated from *A. nitidiuscula* by 1.95% (range 1.95–1.95%), from *A. chrysosceles* by 4.67% (range 4.28–5.06%), and from the other clade of *A. fulvicornis* by 4.18% (range 3.89–4.28%). This Iberian '*fulvicornis*' is also well-supported, with bootstrap support of 96. At the present time, no taxonomic action can be taken until more genetic data are available. Morphologically, Iberian '*fulvicornis*' do not appear to be different from Central European/Turkish/Levantine specimens. Additional sequences from Iberia and France are needed; this barcode difference may be the result of an isolated population in the Iberian glacial refugium.

Subgenus *Plastandrena* Hedicke, 1933

Pisanty et al. (2022b) synonymised the subgenus *Agandrena* with *Plastandrena*, and this broader definition is used here. Some taxonomic problems within this subgenus were discussed by Wood (2023a), who found support for the species-status of *A.* (*Plastandrena*) *nigrospina* Thomson, 1872. Standard barcodes have limited utility for this group for unclear reasons, so care must be taken when interpreting results, as morphologically distinct taxa can form unclear clades, for example *A.* (*Plastandrena*) *tibialis* (Kirby, 1802). This result was reproduced here (Fig. 9), and no further discussion or action is taken; in an Iberian context, members of this subgenus appear to be identifiable using barcodes, but work is needed to revise this group at a Palaearctic scale using more powerful genetic techniques.

***Andrena* (*Plastandrena*) *pilipes* Fabricius, 1781 and *Andrena* (*Plastandrena*) *nigrospina* Thomson, 1872**

Ortiz-Sánchez et al. (2022) reported *A. nigrospina* as new for Spain from the Sierra de Cazorla based on male specimens with their distinctive genital capsule. Wood (2023a) further reported two barcoded specimens from Spain (Sistema Central and Sistema Ibérico) belonging to *A. nigrospina*. This genetic result was further supported with the addition of more sequences from Morocco (Fig. 9), revealing that *A. nigrospina* is also present in the Middle Atlas. The *A. nigrospina* clade maintained a low intraspecific genetic distance of 0.41% (range 0.00–1.06%) from Morocco to Kyrgyzstan, and average separation from *A. pilipes* was 1.63% (range 1.06–2.35%). As this difference is still small in absolute terms, bootstrap support was moderate, with 77 for *A. pilipes* and 84 for *A. nigrospina*, but both are considered to be distinct species. Females cannot currently be consistently separated morphologically, so no characters are given in the identification key. In Iberia, *A. nigrospina* is newly reported for northern Portugal from close to the Peneda-Gerês National Park. The species is likely to be restricted to cooler parts of northern, central, and eastern Iberia where it will probably be found only in mountainous regions, or at least at elevation. More sampling and genetic study is required to define its exact range limits.

Material examined. ***Andrena nigrospina*:** **Portugal:** Minho, Ruivães, N103, 12.v.2019, 1♂, 1♀, leg. Wood, TJWC; **Spain:** Cuenca, Pajaroncillo, 3 km SW, Arroyo de Peña Quebrada, 26.vi.2021, 4♀, leg. T.J. Wood, TJWC (barcoded); Guadalajara, Bustares, 2 km N, Alto Rey, 1780 m, 1♀, 9.vii.2021, leg. T.J. Wood, TJWC (barcoded).

***Andrena* (*Plastandrena*) *agilissima* Scopoli, 1770 and *Andrena* (*Plastandrena*) *asperrima* Pérez, 1895**

Andrena agilissima is a widespread West Palaearctic species that is well-known in Central and Southern Europe to north-western Africa. In contrast, *A. asperrima* is much less well known, having a more Mediterranean distribution in France, Spain, Morocco, Algeria, and Tunisia. Unlike *A. agilissima*, *A. asperrima* is bivoltine and is exceptionally variable in the density, size, and strength of the integumental punctation. In the female sex, the typical form has strong and dense punctures on the terga, allowing easy separation from *A. agilissima* in which the terga have small and subtle punctures. However, many specimens of *A. asperrima* can be found which have greatly reduced tergal punctation and which are therefore extremely similar to *A. agilissima*; they can be separated by the smaller body size and the sparser punctation of the scutum. This sparsely punctate form is more common in the south-west and was described from Morocco by Warncke as *A. asperrima alascana* Warncke, 1974. Overall, the two species are clearly separable by their genital capsules in the male sex.

Because of this variation, it is important to ensure that Iberian material is conspecific with North African material, since the oldest names of Pérez (1895) were described based on North African material. Warncke (1967) designated a male lectotype for

A. asperrima using a specimen from Biskra from the collection of Pic (Fig. 24A, B). This is unjustified, as it is not part of the original syntypic series, and Warncke's designation is here rejected. In Pérez's catalogue, under entry '1030 *Andrena trachodes* J.P.' [an unpublished name; Pérez sometimes changed his mind and therefore a different name to the published name can be present in the catalogue] Pérez writes that the species comes from Constantine [in Algeria], drawing comparison with *A. flessae* Panzer, 1805 (= *A. agilissima* (Scopoli, 1770)) and arguing it differs by the stronger punctation of the metasoma. Inspection of the Pérez collection shows the presence of a female

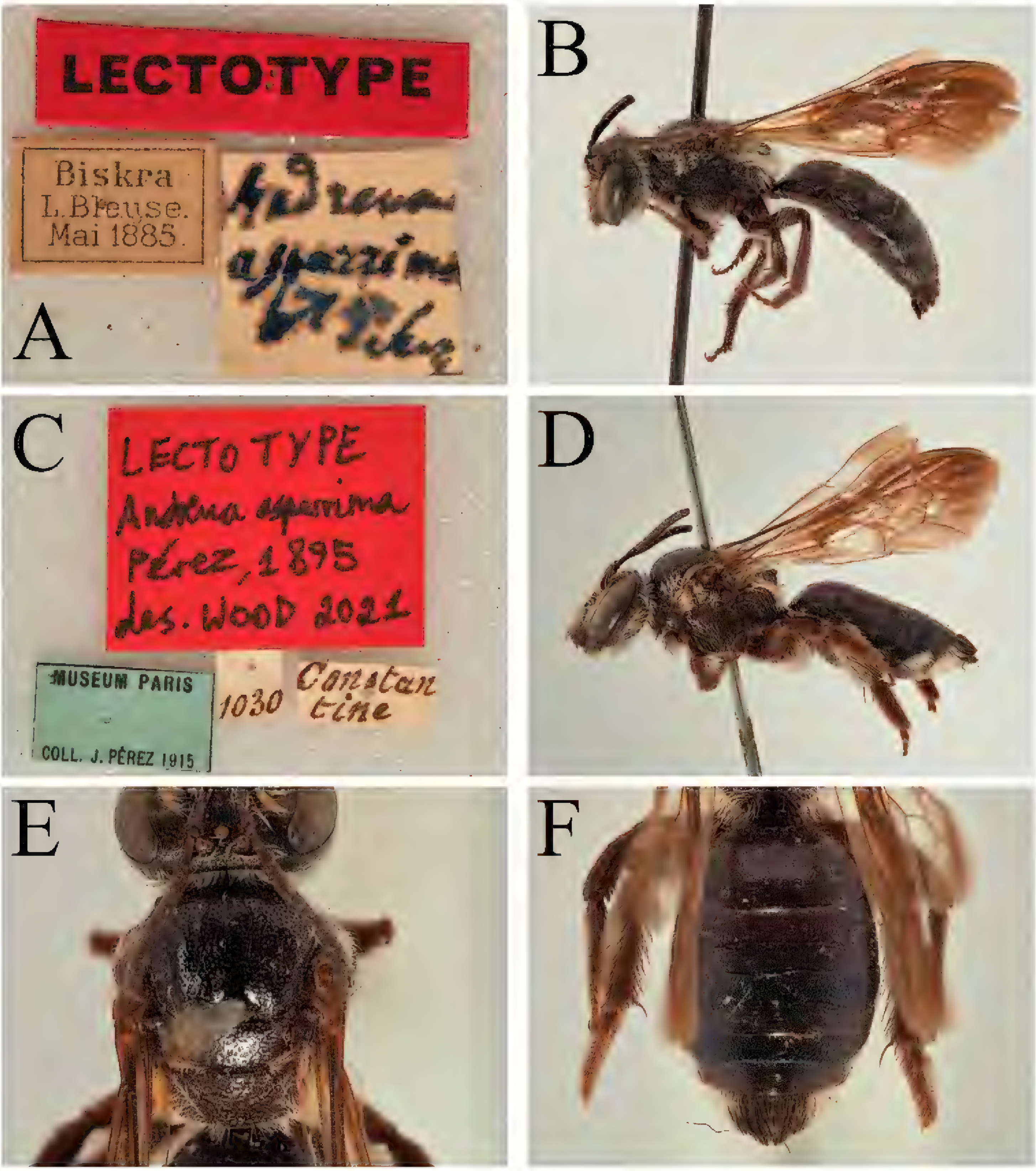

Figure 24. *Andrena* (*Plastandrena*) *asperrima* Pérez, 1895, false male lectotype **A** label details **B** profile; true female lectotype **C** label details **D** profile **E** scutum, dorsal view **F** terga, dorsal view.

specimen from Constantine which bears the label '1030', the code used by Pérez for this species. This specimen is designated as a new lectotype (Fig. 24C–F); it conforms to the concept of *A. asperrima* used by subsequent authors.

Andrena atricapilla Pérez, 1895 was also described from Algeria, but only in the male sex. Warncke (1967) listed this taxon as a synonym of *A. asperrima*, though he did not mention a lectotype. A male specimen labelled as *atricapilla* J.P. in the handwriting of Pérez is separated in the MNHN collection and labelled as a lectotype, probably by Teunissen as one of his determination labels is present. This lectotype designation was never published, and so it is here designated as a lectotype (Fig. 25). The synonymy with *A. asperrima* is maintained, as the genital capsule is typical for the species concept.

Genetic analysis of specimens of *A. agilissima* and *A. asperrima* from Croatia, Morocco, Portugal, and Spain showed two clear clades (Fig. 9). One clade contained only specimens determined as *A. agilissima* from Croatia, Portugal, and Spain. These sequences showed average intraspecific variation of 0.07% (range 0.00–0.25%), and were strongly separated from the second clade by an average genetic distance of 9.33% (range 8.74–10.20%). This second clade contained specimens identified as *A. asperrima* from Spain and Morocco, but also three specimens identified as *A. agilissima* from the Middle Atlas. There can be no doubt as to the identity of these specimens, as two are males, and their genital capsule is that of *A. agilissima* and not *A. asperrima*. However, the genetic differentiation within this clade is very low at an average of 0.42% (range 0.00–0.91%). As for *A. bimaculata* and *A. tibialis*, there is clearly genetic complexity here, as two species with distinct genital capsules have barcodes that form intermixed clades. No taxonomic action is taken on the basis of these barcoding results.

However, what can be concluded is that Iberian material of *A. asperrima* is conspecific with North African material, including the weakly punctate form that dominates in Morocco. In combination with the new lectotype designations, the invariant genital capsule, and these genetic results, the concept of Warncke (1967; 1974) and Gusenleitner and Schwarz (2002) regarding *A. asperrima* is maintained. The full synonymy is given below.

***Andrena* (*Plastandrena*) *asperrima* Pérez, 1895**

Andrena (*Plastandrena*) *asperrima* Pérez, 1895: 33, ♀♂ [Algeria, lectotype by present designation: MNHN].
Andrena (*Plastandrena*) *atricapilla* Pérez, 1895: 33, ♂ [Algeria, lectotype by present designation: MNHN].
Andrena (*Plastandrena*) *flessae* var. *elcheensis* Friese, 1922: 211, ♀ [Spain: ZMHB, not examined].
Andrena (*Plastandrena*) *hemicyanea* Cockerell, 1930: 112, ♀ [Tunisia: type lost?]
Andrena (*Plastandrena*) *asperrima alascana* Warncke, 1974: 36, ♀♂ [Morocco: OÖLM, examined].

Distribution. Spain, France, Morocco, Algeria, Tunisia.

Figure 25. *Andrena* (*Plastandrena*) *atricapilla* Pérez, 1895, male lectotype **A** label details **B** profile **C** terga, dorsal view **D** genital capsule.

Material examined. Algeria: Constantine [36.3645°N, 6.6409°E], 1♀, MNHN (lectotype of *A. asperrima*, by present designation; Fig. 24C–F); Biskra, v.1885, 1♂, leg. Blause, MNHN (false lectotype of *A. asperrima*; Fig. 24A, B); Biskra [34.8600°N, 5.6995°E], 1♂, MNHN (lectotype of *A. atricapilla*, by present designation; Fig. 25); Morocco: Tizi-n-Talrhemt nr. Midelt [32.6821°N, -2.9344°E], 1900 m, 1.vi.1968, leg. M.A. Lieftinck, OÖLM (holotype of *A. asperrima alascana*).

Subgenus *Poecilandrena* Hedicke, 1933

This subgenus is strongly polyphyletic (Pisanty et al. (2022b), but these classification issues relate to eastern taxa; in Iberia, the species belong to *Poecilandrena* s. str. Warncke (1976) listed only one *Poecilandrena* species in Iberia, *A.* (*Poecilandrena*) *labiata* Fabricius, 1781. Ceballos (1956) and Pérez-Íñigo (1984) also listed *A.* (*Poecilandrena*) *potentillae* Panzer, 1809, though this species was not listed as present by Warncke and his distribution maps (Gusenleitner and Schwarz 2002) indicate that this species has a western range limit in central France.

Collection of material from the Sierra Nevada produced red-marked *Poecilandrena* females [WPATW281-21] that morphologically resemble *A. potentillae* in the reduced

punctation density at the edge of the clypeus. No '*potentillae*' males with their distinctive genital capsule could be found. A female sequence clearly fell into a clade with an *A. labiata* sequence from Belgium, the two specimens separated by 2.87% (Fig. 1). The four *A. labiata* sequences from Belgium, Portugal, and Spain showed average intraspecific variation of 2.52% (range 0.78–3.92%), much lower than the average separation from *A. potentillae* sequences from Belgium, France, Germany, and Hungary of 11.81% (range 11.23–12.27%). The position is taken here that true *A. potentillae* is not present in Iberia, even though some females of *A. labiata* can resemble it morphologically. These specimens conform to the subspecific concept of *A. labiata bellina* Warncke, 1967 that was described from Madrid. Warncke (1967) noted that this form had weaker shagreenation and finer punctation than the nominate form, and I believe that this is the source of the confusion and the erroneous reports of *A. potentillae* in Iberia. *Andrena potentillae* is therefore not included in the identification key as typical female characters that can be used to separate the two species in Central Europe do not appear to work universally in Iberia.

Finally, Ortiz-Sánchez (2011, 2020) lists *A.* (*Poecilandrena*) *viridescens* Viereck, 1916 as part of the Spanish fauna. The distribution maps of Warncke (Gusenleitner and Schwarz 2002) indicate the possible presence of this species on the Spanish side of the Pyrenees. I have not examined any specimens of *A. viridescens* from Iberia, but its presence in the Pyrenees is plausible and so it is retained on the list. Several *Andrena* taxa with apparent range limits in the Pyrenees have recently been confirmed to occur in northern Spain (e.g. *A.* (*Ulandrena*) *polita* Smith, 1847 and *A.* (*Micrandrena*) *nanula* Nylander, 1848, see Álvarez Fidalgo et al. 2022), and so additional searches may well confirm the presence of *A. viridescens* as well.

Subgenus *Simandrena* Pérez, 1890

Barcode analysis returned *Simandrena* as paraphyletic (Fig. 4), but this means very little, as the subgenus is very well characterised morphologically and genetically based on UCE analysis (Pisanty et al. 2022b). No major changes in *Simandrena* taxonomy are made here, but there are a number of issues to discuss.

Warncke (1967) described *A.* (*Simandrena*) *combinata crudelis* Warncke, 1967 from Spain. Comparison of sequences shows that Iberian material is only weakly differentiated, being separated from *A.* (*Simandrena*) *combinata* (Christ, 1791) sequences from Germany by an average genetic distance of 1.12% (range 1.06–1.29%). Based on this evidence, a subspecific status is not justified.

Andrena (*Simandrena*) *vetula* Lepeletier, 1841 was recently placed in the *Simandrena*, as its unusual male morphology had led to confused previous placement (Pisanty et al. 2022b). Genetically there was a large difference between Iberian and North African sequences, separated by an average genetic distance of 6.33% (range 6.08–6.57%). *Andrena vetula* has an enormous range, from Morocco and Iberia to Central Asia (Wood and Monfared 2022). Sequences are required over this range before any taxonomic changes can be made, as morphologically there are no obvious differences between Iberian and North African specimens.

The species pair of *A.* (*Simandrena*) *confinis* Stöckhert, 1930 and *A.* (*Simandrena*) *congruens* Schmiedeknecht, 1884 continues to pose problems. Warncke (1967) treated *A. confinis* as a synonym of *A. congruens*, but others have not followed this interpretation. The two taxa can be separated morphologically in Central Europe (Schmid-Egger and Scheuchl 1997), and there are also ecological differences with *A. confinis* preferring cooler northern climates and *A. congruens* preferring warmer and drier southern climates, with overlap in Central Europe. However, in southern Europe the situation is complex and confused. Wood et al. (2021) added *A. confinis* to the Iberian list on the basis of a specimen from the Picos de Europa Mountains. Genetically, this specimen clusters with *A. confinis* sequences from Germany. However, sequences from specimens provisionally identified as *A. congruens* from northern Portugal as well as a specimen of *A. congruens* from Bulgaria render *A. congruens* paraphyletic. The genetic distance between all sequences is low. The Portuguese specimens are strongly divergent morphologically from the Spanish *A. confinis* specimen, with dense and obvious tergal punctation compared to terga which are almost impunctate, but the average genetic differentiation is low at 0.88% (range 0.60–1.15%). No major taxonomic decision is made here; much more genetic data are required for a dedicated study focused on this group. Both nominal taxa are included in the identification key.

Andrena (*Simandrena*) *cilissaeformis* Pérez, 1895, sp. resurr.

Andrena (*Simandrena*) *cilissaeformis* Pérez, 1895: 42, ♀ [Spain, lectotype by present designation: MNHN]
Andrena breviscopa auctorum.

Remarks. *Andrena breviscopa* Pérez, 1895 was described in the female and male sexes from North Africa. Warncke's treatment of *A. breviscopa* is curious, because he designated a lectotype (Fig. 26) and listed the taxon as a synonym of *A. numida* Lepeletier, 1841 (Warncke 1967). However, just a few years later he listed *A. breviscopa* as a valid taxon in the subgenus *Simandrena* (Warncke 1974). Examination of the female lectotype designated by Warncke shows that his original synonymy was correct; the taxon is clearly not a *Simandrena*, and is indeed a synonym of *A. numida*.

The use of the name *A. breviscopa* to apply to the taxon present in Spain, Morocco, and Algeria is therefore incorrect. The correct name is *A. cilissaeformis* Pérez, 1895 sp. resurr. *Andrena cilissaeformis* was described from Spain, not Algeria as stated in Warncke (1967) and Gusenleitner and Schwarz (2002). This is because Pérez (1895) does not directly state the type locality (or indeed, any information about the collecting locality of any of the species described in this work), but this information is included in his personal catalogue. Warncke (1967) did not examine material of *A. cilissaeformis*, stating that whilst the label was present, material was missing. Examination of material in the MNHN has located a specimen labelled with 'Esp' [Espagne = Spain] in Pérez's handwriting (Fig. 27). This specimen was separated by Teunissen, but he never published this information. This specimen is badly damaged, but it is a *Simandrena* and

Figure 26. *Andrena* (incertae sedis) *breviscopa* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

conforms to *A. breviscopa* auctorum sensu Warncke (1974) and subsequent publications. It is designated as a lectotype to fix the name on the Iberian population. *Andrena breviscopa* is returned to its original synonymy with *A. numida*.

Distribution. Spain, Morocco, Algeria.

Material examined. ***Andrena breviscopa*:** **Algeria:** Ghardaia [32.5047°N, 3.6419°E], 1♀, MNHN (lectotype; Fig. 26); (*Andrena cilissaeformis*): **Spain:** no collection information, 1♀, MNHN (lectotype by present designation; Fig. 27).

Subgenus *Taeniandrena* Hedicke, 1933

Large parts of this subgenus have been revised recently by Wood et al. (2021), Praz et al. (2022), Wood (2022), and Wood and Ortiz-Sánchez (2022). There is relatively little new information to present here, other than to revise the status of *A.* (*Taeniandrena*) *poupillieri* Dours, 1872, and so a reduced phylogenetic tree is presented given the results presented in these previous publications (Fig. 28). However, it is clear that there is still unfinished work to be completed in this subgenus in an Iberian context. Specifically, Praz et al. (2022) identified an unclear lineage "*sp. nov. 2*" from northern Portugal. This specimen is a male that has a genital capsule that diverges from any known Iberian

Figure 27. *Andrena* (*Simandrena*) *cilissaeformis* Pérez, 1895; female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

species. Furthermore, I have an unbarcoded male from Guadalajara province that also possesses a genital capsule that does not match any known species. These may represent additional undescribed *Taeniandrena* species endemic to the peninsula. No further action is taken until more genetic samples are available; it is extremely likely that additional barcoding will discover more diversity in this challenging and speciose subgenus.

Andrena (*Taeniandrena*) *poupillieri* Dours, 1872

Two further issues require discussion. The first is the identity of *A. poupillieri*. Praz et al. (2022) identified two potential mitochondrial lineages that could correspond to this species. Additional sampling in Morocco has clarified the situation; *poupillieri 1* sensu Praz et al. (2022) corresponds to *A.* (*Taeniandrena*) *gregaria* Warncke, 1974 and *poupillieri 2* sensu Praz et al. (2022) corresponds to the concept of *A. poupillieri* used by Warncke. As the type of *A. poupillieri* is lost, it is beneficial to designate a neotype in order to fix the concept of this species in line with the existing literature; a specimen from Algeria is chosen, as this is the original *locus typicus*. As *A. gregaria* does not occur in Iberia, it is not included in the phylogenetic tree presented here; it will be dealt with in the upcoming North African *Andrena* revision. The species *A. poupillieri* is

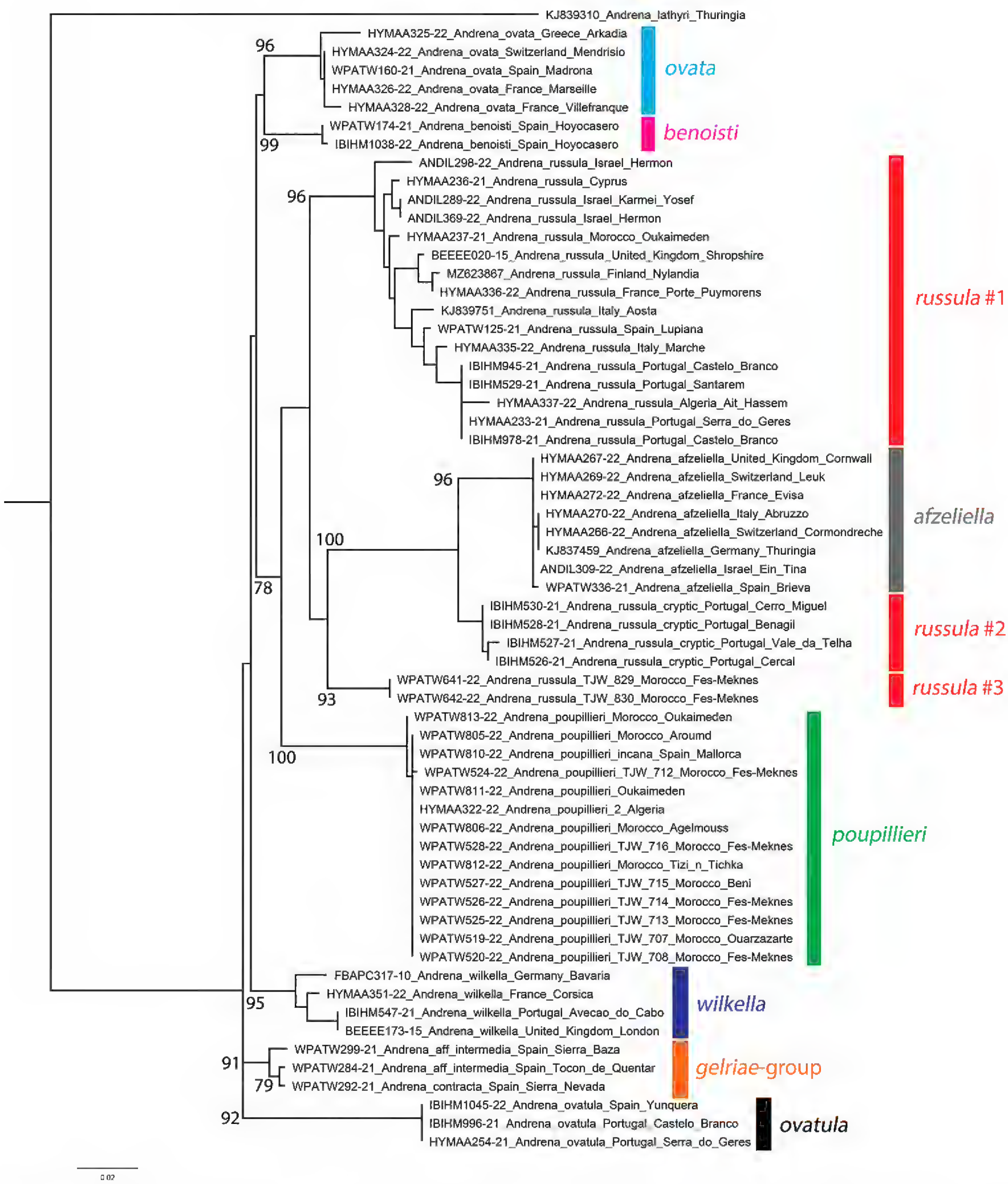

Figure 28. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Taeniandrena* Hedicke, 1933 based on the mitochondrial COI gene. *Andrena* (*Taeniandrena*) *lathyri* Alfken, 1900 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

commonly encountered in Morocco, and is clearly identifiable from barcodes, forming a clade with bootstrap support of 100. Separation of females from *A.* (*Taeniandrena*) *ovatula* (Kirby, 1802) can be made by the tergal punctation, this being much stronger in *A. ovatula*. Generally, the two taxa are well-separated by an average genetic distance of 6.12% (range 5.86–7.79%). Males of *A. poupillieri* can be recognised based on the genital capsule, in which the gonostyli are apically produced into acute points.

Warncke changed his mind about the status of *A. poupillieri* – in Warncke (1967), he lists the taxon as *A. ovatula poupillieri*, but then in Warncke (1975a) he described *A. poupillieri incana* from the Balearic islands, listing *A. poupillieri* s. str. from southern Iberia (Warncke 1976). In his distribution maps (Gusenleitner and Schwarz 2002), he gives a distribution of southern Iberia, the Balearic islands, north-western Africa, Libya, and Crete. Records from Crete are likely to refer to unrecognised *A.* (*Taeniandrena*) *ovata* Schenck, 1853 (Wood, unpublished data). Examination of male specimens from the extreme south of Spain shows that *A. poupillieri* is present based on the distinctive genital capsule, though as females cannot be separated morphologically from *A. ovatula* the exact range of the two species is unclear. *Andrena ovatula* reaches at least as far south at the Sierra de las Nieves in Málaga province [IBIHM1045-22], though this far south it may be restricted to mountainous areas whereas the two examined male *A. poupillieri* specimens come from the coast. More collection is required. For now, *A. poupillieri* is considered to be a rare and little-collected taxon in Iberia, probably restricted to the coast in the south and south-east of the peninsula. A single sequence for *A. p. incana* was available from Mallorca that unambiguously nests within the North African *A. poupillieri* sequences; it is identical to 12 of the North African sequences, and differs from the thirteenth by just 0.15%. As such, *A. poupillieri* including *A. p. incana* shows extremely low intraspecific variation of 0.03% (range 0.00–0.15%), and subspecific status is unnecessary for the population on the Balearic islands.

Material examined. **Spain:** Málaga, Estepona, 24.iii.1986, 1♂, leg. J. van Oosterhout, RMNH; Málaga, San Pedro de Alcántara, 15.iii.1986, 1♂, leg. C. v. Achterberg, RMNH.

Andrena (*Taeniandrena*) *russula* Lepeletier, 1841

Praz et al. (2022) synonymised *A.* (*Taeniandrena*) *similis* Smith, 1849 with *A. russula*, taking a broad, pan-Mediterranean approach. In an Iberian context, sequences from central and northern Iberia clearly fall into a broad *A. russula* clade along with sequences from Morocco to Cyprus and Israel and north to the United Kingdom and Finland (Fig. 28). However, in the extreme south-west of Iberia in southern Portugal, sequences from specimens that are morphologically indistinguishable from *A. russula* from the rest of Iberia form a distinct clade that falls closest to *A.* (*Taeniandrena*) *afzeliella* (Kirby, 1802). These specimens come from the south of Baixo Alentejo (Cercal) and the Algarve (Aljezur, Benagil, Moncarapacho). These sequences are consistently separated from the broad *A. russula* clade by 5.50% (range 3.68–11.11%). Two specimens from Morocco that correspond to *A. russula* form a third clade of *A. russula* s.l. At the present time, no taxonomic action is taken; these three lineages may represent different isolated populations. More powerful genetic techniques are required to resolve this problem, as for Iberian members of the *gelriae*-group (see Praz et al. 2022).

Andrena (*Taeniandrena*) *gredana* Warncke, 1975

Wood et al. (2021) elevated *A. gredana* to species status, and gave a distribution across the Sistema Central, central and northern Portugal, and northern Spain across to the

Pyrenees in the province of Huesca. Examination of material from the Hautes-Pyrénées in France approximately 80 km north-east of the Huesca site revealed the presence of *A. gredana* in France. The species is therefore not endemic to the Iberian Peninsula, though it is likely to have a French range restricted to high altitude sites in the Pyrenees.

Material examined. France: Hautes-Pyrénées, Eget Cité, 4.v.2017, 1♂, leg. R. Rudelle, R. Rudelle Colln.; **Spain:** Huesca, San Juan de la Peña, 14.v.1995, 1♂, leg. H. & J.E. Wiering, RMNH (see also records in Wood et al. 2021).

Subgenus *Truncandrena* Warncke, 1968

This subgenus contains species that often vary extensively in the colouration of their pubescence, sometimes display minimal variation in structural characteristics in the female sex, and can sometimes only be reliably identified in the male sex. These identification difficulties have led to a large number of subspecific concepts in the literature, the integrity of which must be examined using molecular data. There are a number of taxonomic changes to make which affect the Iberian and more broadly West Mediterranean fauna.

Andrena (*Truncandrena*) *doursana* Dufour, 1853 sensu lato

This nominal species is highly variable across its range which was previously considered to be from Morocco and Iberia to Turkey and the Levant. *Andrena doursana* was originally described from Algeria, and Warncke (1975a, 1975b, 1980) described the subspecies *A. d. citreola* Warncke, 1975 from Spain, *A. d. agadira* Warncke, 1980 from southern Morocco, *A. d. bengasia* Warncke, 1980 from Libya, and *A. d. mizorhina* Warncke, 1975 from Turkey. Pisanty et al. (2022b) elevated the eastern subspecies *A.* (*Truncandrena*) *doursana mizorhina* to species status, leaving populations in Iberia and north-western Africa to Libya.

The differentiation between these remaining subspecies relies on the colour of the female pubescence, as there are no structural differences in the males; indeed, the subspecies *A. d. agadira* and *A. d. bengasia* were described only from the female sex. *Andrena d. citreola* is bright, and has predominantly white hairs on the face and a light brown terminal fringe with scattered white hairs laterally. *Andrena d. agadira* is much darker, with dark facial hairs and a uniformly dark terminal fringe. Wood et al. (2020b) found the undescribed female of a similar species endemic to Morocco, *A.* (*Truncandrena*) *alchata* Warncke, 1974, which is structurally very similar to the female of *A. d. agadira*, but these authors were unable to conclude if the two taxa were synonymous.

Analysis of barcodes from southern and northern Morocco and Iberia shows that female specimens identified as *A. doursana* s. str., *A. d. agadira*, and *A. d. citreola* did not form differentiated clades (Fig. 29). Light forms from southern Portugal [IBIHM1223-22] and the Moroccan Anti-Atlas near Tazenakht [WPATW505-22] were separated, and dark forms from south-western Morocco near Guelmim [WPATW506-22] and Tiznit [WPATW503-22] were clustered closer to the light specimen from Tazenakht. The light specimen from Portugal was clustered close to

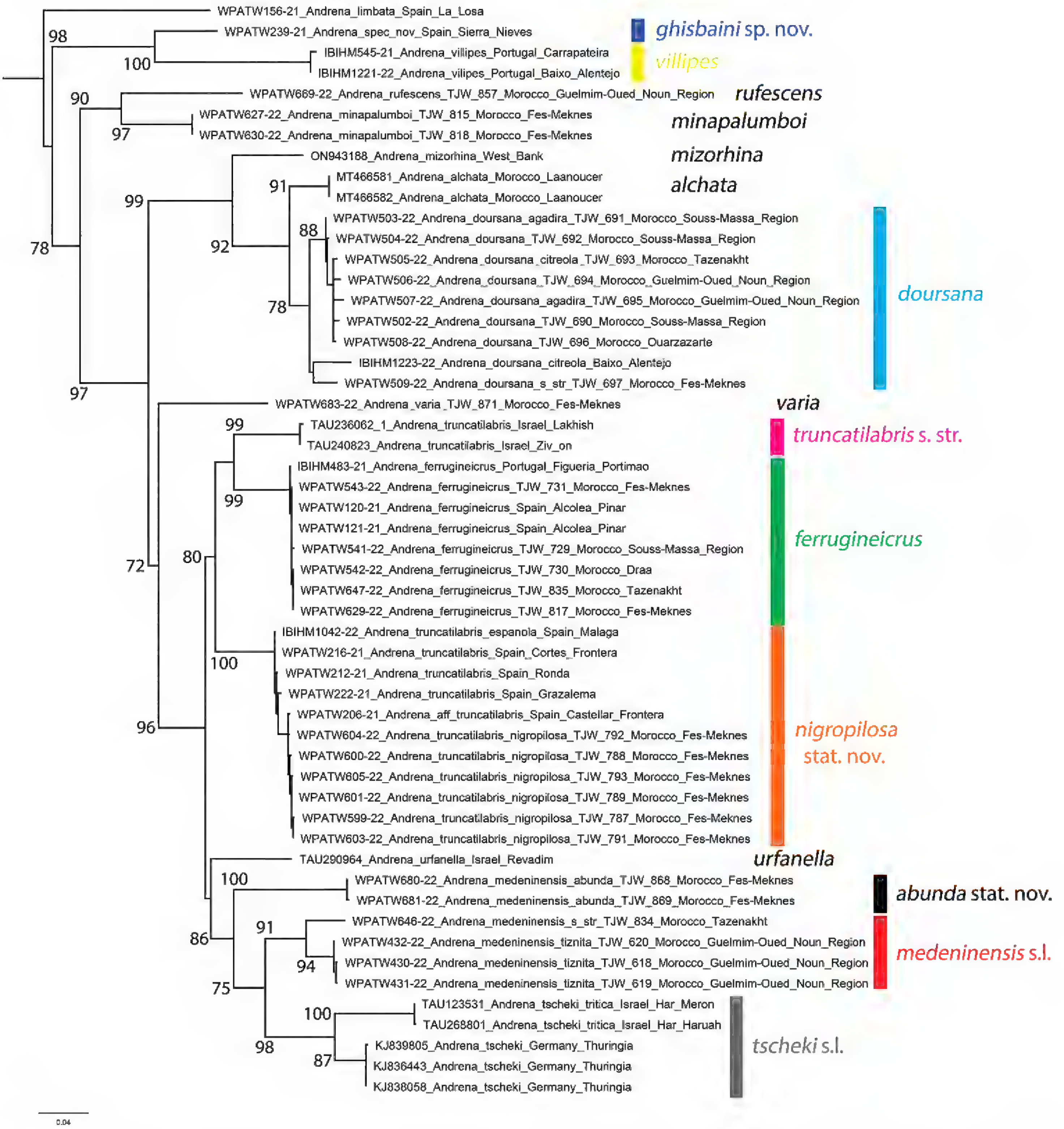

Figure 29. Phylogenetic tree (maximum likelihood) of *Andrena* subgenus *Truncandrena* Warncke, 1968 based on the mitochondrial COI gene. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

a specimen of *A. doursana* s. str. from the Middle Atlas near Taza [WPATW509-22]. This pattern strongly suggests simple separation by distance, with geographically closer specimens displaying more similar barcode sequences. Accepting a broad *A. doursana* species concept, these sequences showed an average intraspecific distance of 2.79% (range 0.29–5.93%).

More broadly, this *A. doursana* clade had bootstrap support of 78, and was sister to the *A. alchata* sequences generated by Wood et al. (2020b), a species that has a clearly different male morphology. *Andrena alchata* has bootstrap support of 91, and was

separated from *A. doursana* by an average of 6.29% (range 5.62–8.03%). Finally, the single sequence of *A. mizorhina* was strongly separated from *A. doursana* by an average of 10.45% (range 10.18–10.94%). These genetic results justify the decision of Pisanty et al. (2022b) to elevate *A. mizorhina* to species level, the findings of Wood et al. (2020b) who identifed the female of *A. alchata*, and the original description of *A. d. agadira* by Warncke as a subspecies, correctly associating dark specimens from south-western Morocco with *A. doursana*. Given the variation in colour forms observed here, no subspecies framework is employed, and so the Iberian taxon is referred to simply as *A. doursana*.

***Andrena* (*Truncandrena*) *medeninensis* Pérez, 1895 sensu lato**

Andrena medeninensis was described from Tunisia, and like *A. doursana*, it nominally displays great variation across its range from Morocco and Iberia to Turkey and the Levant. Warncke (1967, 1974, 1980) described several subspecies, *A. m. donata* Warncke, 1967 from Spain, *A. m. abunda* Warncke, 1974 from Morocco, *A. m. tiznita* Warncke, 1980 from south-western Morocco, and *A. m. usura* Warncke, 1967 from Turkey. Wood (2023b) synonymised *A. m. usura* with *A. pareklisiae* Mavromoustakis, 1957, leaving the North African and Iberian populations.

Sequences of *A. medeninensis* s. str. and *A. m. tiznita* formed a clade with bootstrap support of 91 (Fig. 29). However, the single available sequence of *A. medeninensis* s. str. differed from *A. m. tiznita* sequences by an average of 4.80% (range 4.70–4.85%), *A. m. tiznita* forming a subclade with bootstrap support of 94. However, *A. m. abunda* was strongly separated from this clade of *A. medeninensis* s.l. by an average genetic distance of 10.19% (range 9.97–10.57%). This *A. m. abunda* clade had bootstrap support of 100, and was sister to an *A. medeninensis* s.l. + *A. tscheki* Morawitz, 1872 s.l. clade. *Andrena abunda* stat. nov. is therefore raised to species status; it restricted to Algeria and Morocco. Morphologically, it is extremely similar to *A. medeninensis* s.l., but has much darker pubescence. In the female sex (the male is unknown), the only clear structural difference is that A3 exceeds the length of A4+5+6, whereas in *A. medeninensis* s.l. A3 is shorter than A4+5+6.

As it was unfortunately not possible to sample the Iberian subspecies *A. m. donata*, and no genetic sequences are available from Tunisia, the *locus typicus* for *A. medeninensis* s. str., no further taxonomic action is taken here. Given the large genetic difference displayed by *A. abunda* despite almost no morphological differentiation (at least in the female sex), it is difficult to comment on the Iberian subspecies which simply appears to be a colour variant of this nominally widespread species.

***Andrena* (*Truncandrena*) *truncatilabris* Morawitz, 1877, *Andrena* (*Truncandrena*) *truncatilabris espanola* Warncke, 1967, and *Andrena* (*Truncandrena*) *truncatilabris nigropilosa* Warncke, 1967**

Andrena truncatilabris is a widespread species that was originally described from the Caucasus from what is today Armenia (Astafurova et al. 2021). The species is nominally

distributed across the Mediterranean basin, from Morocco and Iberia to the Urals and Iran (Gusenleitner and Schwarz 2002). However, in the east it descends only to the Levant and does not enter the eastern part of North Africa. In the west, Warncke (1967) described two subspecies: *A. t. espanola* from Spain and *A. t. nigropilosa* from Algeria that differed from *A. truncatilabris* s. str. in the structure of their clypeus and their male genital capsule, though Warncke noted that the difference between the two subspecies was minimal, pointing to the darker pubescence of North African specimens as a point of difference.

Sequences from specimens from Spain and Morocco showed almost no genetic differentiation, with an average intraspecific distance of 0.99% (range 0.00–1.85%; Fig. 29). They were strongly separated from *A. truncatilabris* s. str. sequences from northern Israel by an average genetic distance of 9.66% (range 9.12–10.12%). *Andrena truncatilabris* s. str. formed a clade with bootstrap support of 99, and was sister to *A.* (*Truncandrena*) *ferrugineicrus* Dours, 1872, whereas *A. t. nigropilosa* + *A. t. espanola* formed a clade with bootstrap support of 100 that was sister to the *A. truncatilabris* s. str. + *A. ferrugineicrus* clade.

Given this genetic difference, it is clear that specimens from Iberia and north-western Africa are both conspecific and distinct from *A. truncatilabris* s. str. Given this distribution, the use of the name *A. t. espanola* is undesirable, and so *A. nigropilosa* stat. nov. is elevated to species status and *A. t. espanola* syn. nov. is synonymised with it as a subjective junior synonym, as the two names were described in the same publication. The updated synonymy is therefore as follows:

***Andrena* (*Truncandrena*) *nigropilosa* Warncke, 1967, stat. nov.**

Andrena (*Truncandrena*) *truncatilabris nigropilosa* Warncke, 1967: 225, ♀♂ [Algeria: OÖLM, examined].

Andrena (*Truncandrena*) *truncatilabris espanola* Warncke, 1967: 224, ♀♂ [Spain: OÖLM, examined] syn. nov.

Distribution. Portugal, Spain, France, Morocco, Algeria, Tunisia (newly recorded). Material from south-eastern France and northern Italy must be carefully revised, but the position is taken here that the Maritime Alps represent a barrier between *A. nigropilosa* and *A. truncatilabris* s. str. This should be confirmed with genetic evidence.

Material examined. **Algeria:** S. Algeria, Laghouat [33.8082°N, 2.8316°E], iii.–iv.1929, 1♀, leg. Meyer, OÖLM (holotype of *A. t. nigropilosa*); Tlemcen, 20.iv.1910, 1♂, leg. de Bergeoin, OÖLM (paratype of *A. t. nigropilosa*); **Spain:** Sierra Nevada [37.0732°N, -3.3948°E], vi.1891, 1♀, leg. Handl., OÖLM (holotype of *A. t. espanola*); Montarco, 28.iv.1924, 1♂, leg. J.M. Dusmet y Alonso, OÖLM (paratype of *A. t. espanola*); **Tunisia:** Kef, 5 km SW Touiref, 28.iv.2012, 41, leg. C. Sevidy & A. Müller, AMC/TJWC.

***Andrena* (*Truncandrena*) *villipes* Pérez, 1895**

Pérez (1895) described *A. villipes* from north-eastern Spain (Fig. 30), later describing the synonymous *A.* (*Truncandrena*) *squalida* Pérez, 1903 from south-western

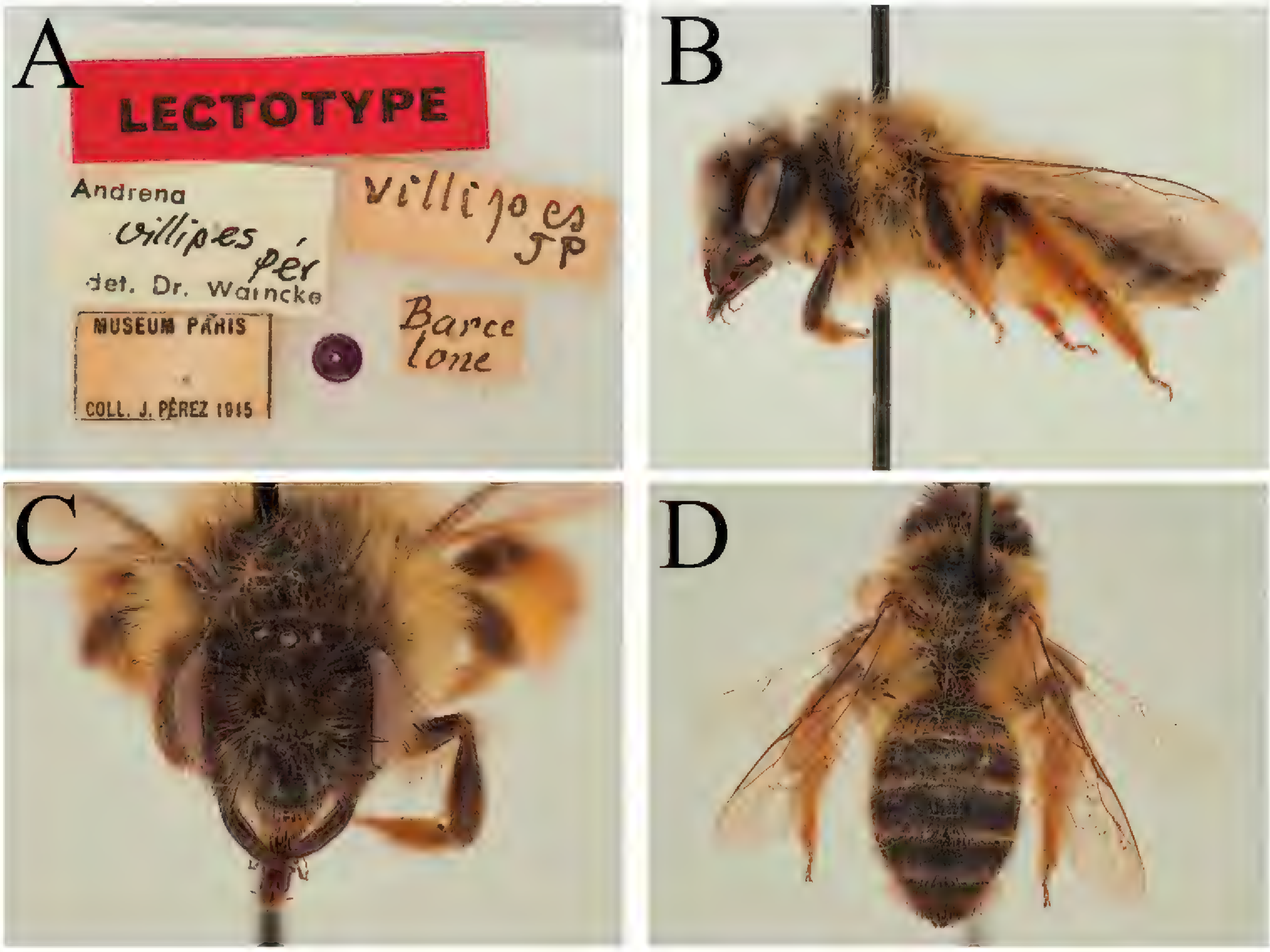

Figure 30. *Andrena* (*Truncandrena*) *villipes* Pérez, 1895; female lectotype **A** label details **B** profile **C** face, frontal view **D** dorsal view.

France. It has a restricted distribution, known from Cistaceae-rich habitats from northern Morocco, Portugal, Spain, southern France, and north-western Italy (Gusenleitner and Schwarz 2002; Lhomme et al. 2020). Searches in the Sierra de las Nieves in southern Spain produced two particularly large and dark specimens provisionally identified as *A. villipes*. A sequence from one of these specimens is separated from *A. villipes* sequences from southern Portugal by an average genetic distance of 11.85% (range 11.85–11.85%). This new species is described and diagnosed below.

Material examined. Spain: Barcelona [41.4028°N, 2.1332°E], 1♀, MNHN (lectotype of *A. villipes*; Fig. 30).

Undescribed subgenera

As a result of the ground-breaking analysis of Pisanty et al. (2022b), we now have unprecedented phylogenetic resolution for the genus *Andrena*, and are now able to seriously deal with the problems inherent to the subgeneric classification system largely solidified by Warncke (1968a). Building on the work of Pisanty et al. (2022b), the Iberian fauna contains representatives of 44 described subgenera, but also representatives for nine additional clades that are currently undescribed. Some of these are dealt with

here, though the *aegyptiaca*-group (Iberian representative: *A. alluaudi* Benoist, 1961) is not treated here; this lineage will be described in a planned future comprehensive revision of the subgenus.

The former *Poliandrena* Warncke, 1968

Pisanty et al. (2022b) demonstrated that *Andrena polita* Smith, 1847 falls into an expanded *Ulandrena*, and that *Poliandrena* is a strict synonym of this subgenus, and additionally that *Poliandrena* sensu Warncke contains at least five different polyphyletic clades, with the possibility of additional distinct clades when taxonomic sampling and phylogenetic analysis is more complete. Warncke, who described the subgenus *Poliandrena*, understandably used it as a 'waste-basket' for unclear taxa that displayed no clear defining characters. It is therefore necessary to split up this old grouping and to describe new subgenera.

In Iberia, representatives of all five subgenera can be found. These can be broadly summarised as the *blanda*-group, the *florea*-group, the *limbata*-group, the *oviventris*-group, and the *relata*-group. Four of these five lineages are represented in the analysis of Pisanty et al. (2022b) which is based on UCE analysis. UCE analyses are based on thousands of loci, and hence offer a high degree of confidence that groups are or are not related. Whilst single locus COI analyses cannot compare to those based on UCEs, they can demonstrate if individual species are closely related, and hence complement a UCE-informed phylogeny. No members of the *oviventris*-group were included in the analysis of Pisanty et al. (2022b), but analysis of barcodes (Fig. 31) places *A. farinosa* Pérez, 1895, *A. farinosoides* Wood, 2020, and *A. oviventris* Pérez, 1895 in a single clade with bootstrap support of 99, well-separated from *A. corax* Warncke, 1975, *A. murana* Warncke, 1975, and *A. relata* Warncke, 1975 which belong to the *relata*-group and which are morphologically the most similar to members of the *oviventris*-group. The two clades are separated by *A. limbata* Eversmann, 1852. On the basis of the analysis of Pisanty et al. (2022b) combined with these barcodes, subgenera are described for the *blanda*-group, *florea*-group, *limbata*-group, and *oviventris*-group.

No action is currently taken for members of the *relata*-group, as the status of morphologically similar species in the Eastern Mediterranean to Central Asia is unclear, and it must be genetically demonstrated if they belong to the *relata*-group or not. The members of the newly described subgenera are detailed below; in an Iberian context, the following species can be considered to be part of the *relata*-group: *A. corax*, *A. laurivora* Warncke, 1974, *A. macroptera* Warncke, 1974, *A. murana*, and *A. relata*.

The *caroli*-group

Members of this group of species have been placed in the subgenus *Campylogaster* Dours, 1873 (Warncke 1968a) that has the type species *A. erberi* Morawitz, 1871. Pisanty et al. (2022b) identified that *Campylogaster* is polyphyletic, with *A. caroli* Pérez, 1895 falling far away from *A. erberi*. *Campylogaster* therefore can probably only be

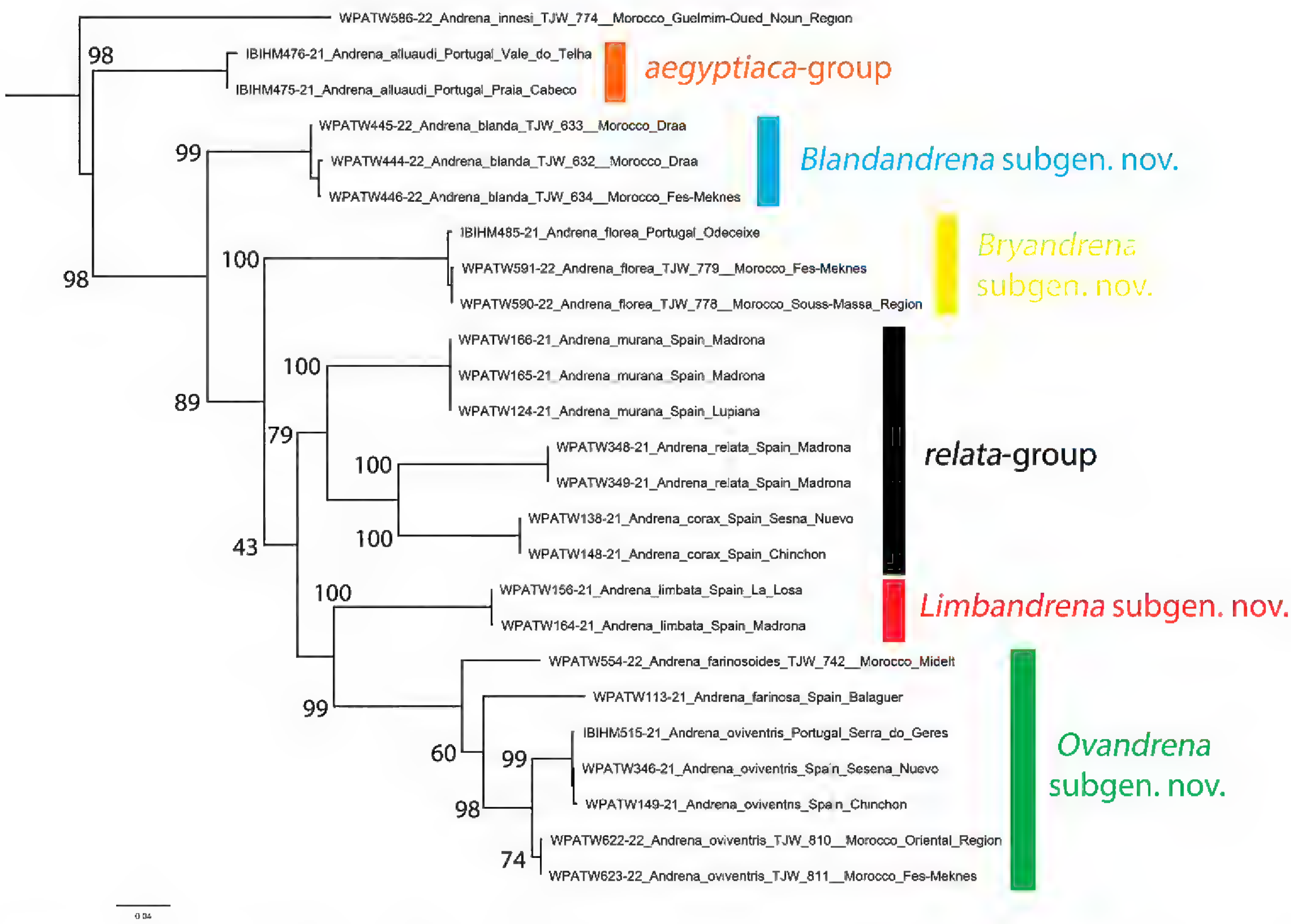

Figure 31. Phylogenetic tree (maximum likelihood) of *Andrena* from currently undescribed subgenera based on the mitochondrial COI gene. *Andrena* (incertae sedis) *innesi* Gribodo, 1894 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

applied to the species around *A. erberi* that have strongly depressed tergal margins, e.g. *A. iranella* Popov, 1940 (Iran, Turkemenistan, ?Arabian Peninsula), *A. nanshanica* Popov, 1940 (China, Mongolia), *A. chengtehensis* Yasumatsu, 1935 (China, South Korea). This subgenus therefore appears to be eastern and predominantly Asian, with a western limit of *A. erberi* in the southern Balkans. In contrast, *A. caroli* has the tergal margins flat and not noticeably depressed. Based on the analysis of Pisanty et al. (2022b) combined with this morphological difference, a new subgenus *Pruinosandrena* subgen. nov. is described below for the species around *A. caroli*. Importantly, *A. lateralis* Morawitz, 1876 and *A. incisa* Eversmann, 1852 were also placed into *Campylogaster* by Warncke (1968a). Although not sampled by Pisanty et al. (2022b), *A. lateralis* falls far away from the *Pruinosandrena* based on COI analysis (Fig. 32). Morphologically, *A. lateralis* and *A. incisa* form a species pair (that can be referred to at the *incisa*-group) that lacks many of the characters shared by members of the *Pruinosandrena* (see below), and they probably represent an additional undescribed subgenus. Without additional genetic data, no further steps are taken for this species pair at the present time.

Finally, clarity is required for the status of taxa lumped under a broad concept of *A. pruinosa* Erichson, 1835, specifically *A. pruinosa succinea* Dours, 1872 and *A. pruinosa parata* Warncke, 1967. Erichson (1835) described *A. pruinosa* from southern Spain

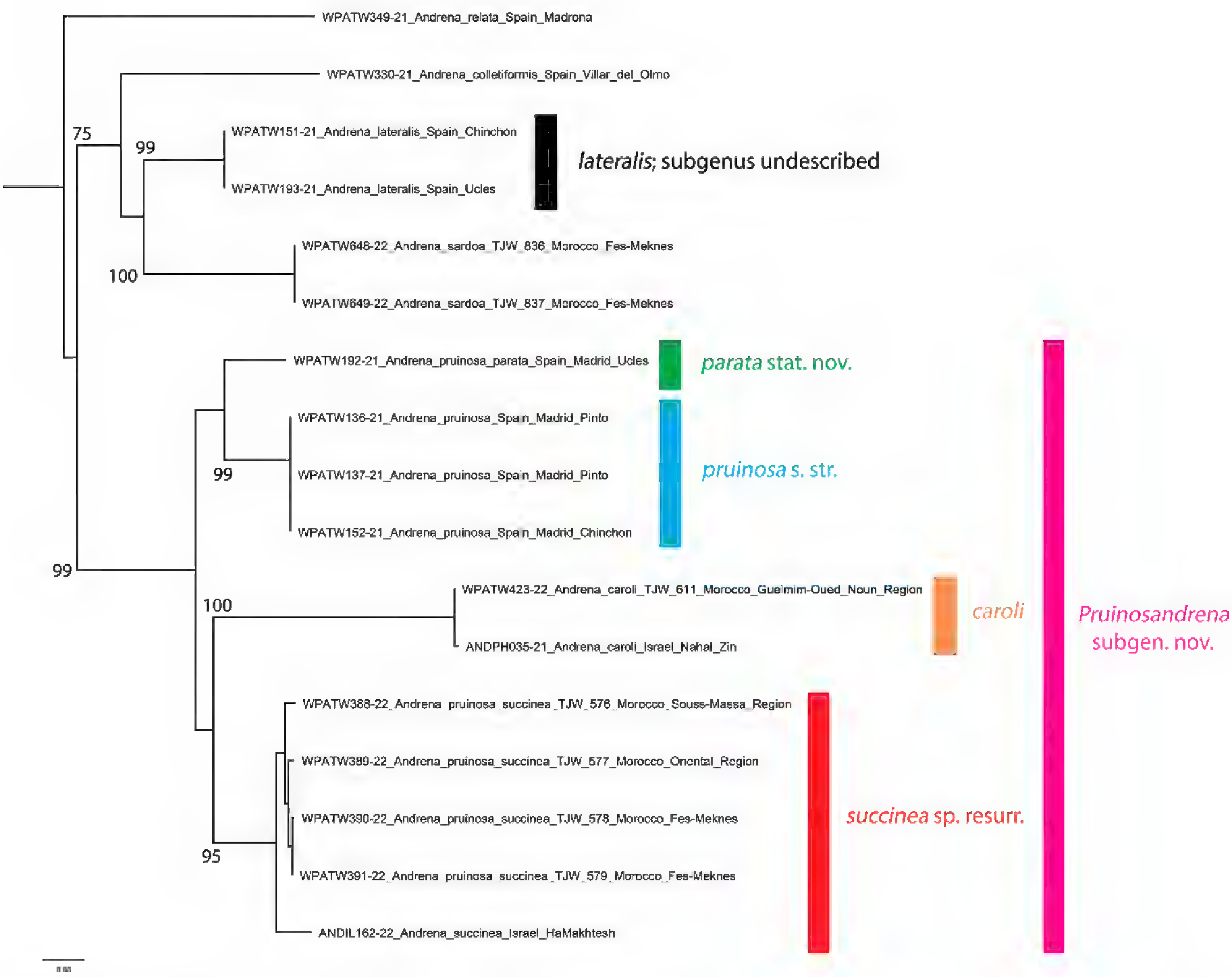

Figure 32. Phylogenetic tree (maximum likelihood) of *Andrena* from the subgenera *Brachyandrena* Pittioni, 1948, *Lepidandrena* Hedicke, 1933, and currently undescribed subgenera based on the mitochondrial COI gene. *Andrena* (incertae sedis) *relata* Warncke, 1975 is used as an outgroup. Numbers adjacent to branches represent bootstrap support (values of <75 are omitted).

(Andalusia); a single female labelled as 'type' is conserved in the ZMHB which may automatically be the holotype (Fig. 33), but this is ambiguous as it is unclear if Erichson described the species from multiple specimens or not. Dours (1872) described *A. succinea* from Algeria, noting the clear red colouration of the metasoma (hence the species name, *succin* = amber). Warncke (1967) used *A. succinea* as a subspecies in combination with *A. pruinosa*, arguing that males from North Africa could not be clearly separated from Spanish males. He then described *A. pruinosa parata* from south-eastern Spain, giving characters related to colouration and antennal ratios.

Genetic analysis of members of the *Pruinosandrena* demonstrates that the broad concept of *A. pruinosa* used by Warncke was overly conservative (Fig. 32). A single red-marked female specimen initially identified as *A. pruinosa* was separated by 7.45% from three additional *A. pruinosa* s. str. specimens. Inspection of Warncke's original description of *A. pruinosa parata* and comparison of the antennal ratios demonstrates that this divergent specimen has A3 clearly longer than A4+5, whereas A3=A4+5 in *A. pruinosa* s. str. The other characters mentioned by Warncke relating to colour do not

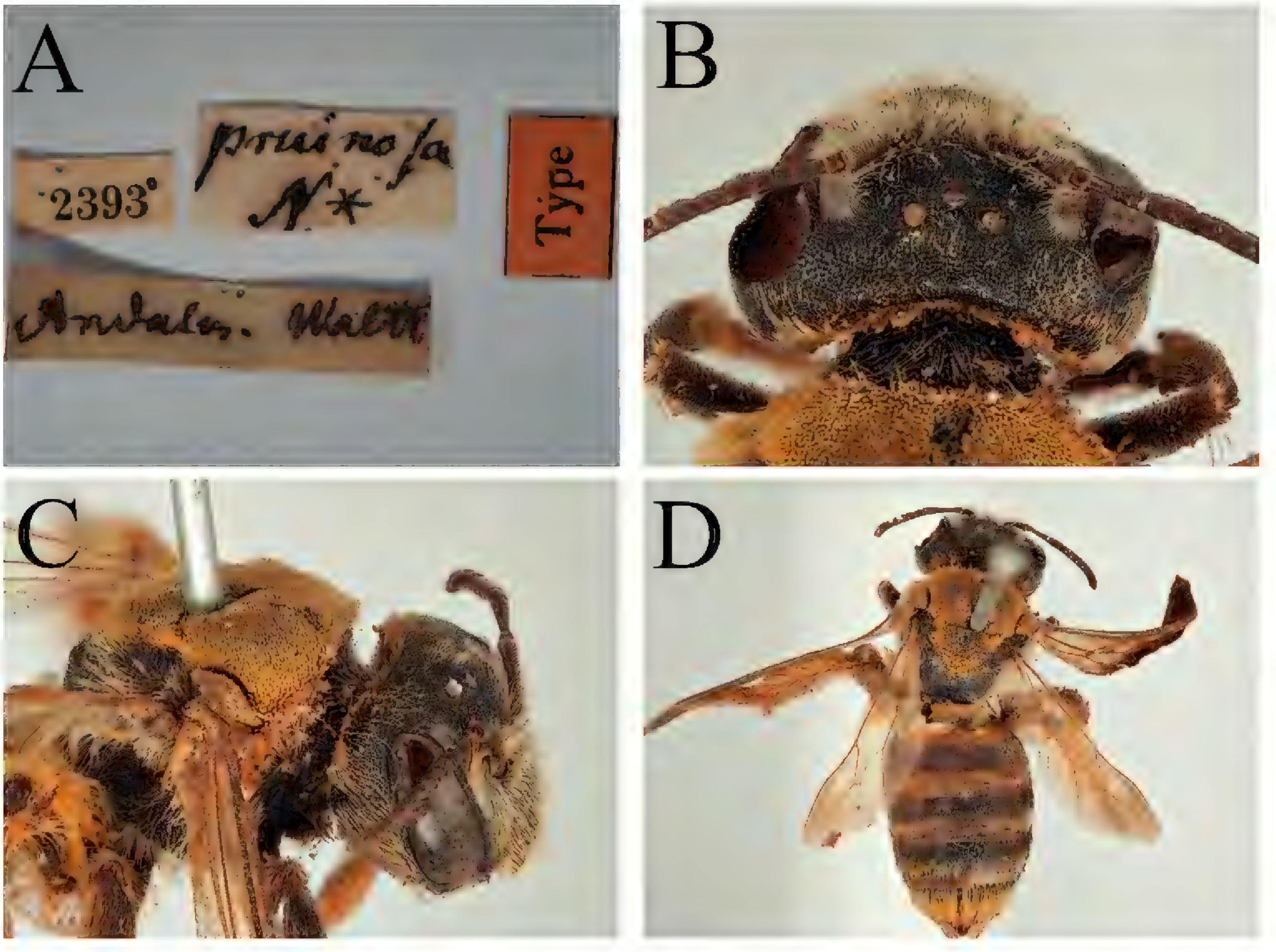

Figure 33. *Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835, female holotype/syntype **A** label details **B** head, dorsal view **C** mesosoma, dorsolateral view **D** dorsal view.

work consistently, as one of the barcoded *A. pruinosa* s. str. has the terga partially red-marked and the hind tibiae lightened orange. Though small, this morphological difference is meaningful, as the two taxa are found essentially in direct sympatry; the distance between the sampling location of barcoded specimens of *A. pruinosa* s. str. from Pinto was approximately 11 km from the Camino de Uclés sampling site for *A. pruinosa parata*. In this context, a genetic separation of 7.45% combined with the morphological difference is highly significant, and *A. parata* stat. nov. is treated as a valid species.

Andrena pruinosa succinea was strongly separated from *A. pruinosa* s. str. by an average genetic distance of 9.45% (range 8.97–10.33%). Sequences of *A. pruinosa* s. str. were identical, which is not surprising as they all came from a small part of the province of Madrid. *Andrena pruinosa succinea* samples came from a large geographic area from south-western Morocco to Israel, but still showed low average intraspecific variation of 2.06% (range 0.14–3.80%). The two clades were not sister, being separated by *A. parata* and *A. caroli*, and were supported by bootstrap support of 99 and 95, respectively. *Andrena succinea* sp. resurr. is therefore considered to be a valid species, distinct from *A. pruinosa* s. str. Morphologically, separation of males is straightforward, and it is unclear why Warncke considered the difference unclear. *Andrena succinea* males have a yellow marked clypeus (see illustrations in Wood et al. 2020b), with the yellow

markings sometimes extending onto the lower part of the paraocular areas (uniformly black in *A. pruinosa* s. str. and *A. parata*) and, viewed ventrally, A4 is short, as long as broad (A4 is elongate and clearly longer than broad in *A. pruinosa* s. str.). *Andrena parata* males can easily be separated as A3 is longer than A4+5, whereas A3 is shorter than A4+5 in both *A. pruinosa* s. str. and *A. succinea*.

There are also ecological differences. *Andrena succinea* can be found in dry desert-edge steppe habitats, as opposed to *A. pruinosa* which in Iberia is found in grasslands and cold steppe that are lightly more lush, at least during the spring. For example, in Morocco, *A. succinea* can be found in stipa steppe habitat around Bou Rached (Oriental region, south of Guercif) on the eastern edge of the Middle Atlas as it transitions into the desert (Fig. 34A, B), whereas it has never been recorded from the more humid parts of the Middle Atlas that have grasslands resembling those that can be found in central Iberia (e.g. Madrid, north of Chinchón, Fig. 34C, D).

Although the type of *A. succinea* is lost, and the type for a more recently described taxon is preserved in the MNHN collection (*A. sitifensis* Pérez, 1895; Fig. 35), *A. succinea* is the name that is established in the literature, either as a species itself or in combination with *A. pruinosa* (Benoist 1961; Warncke 1967; Warncke 1974; Gusenleitner and Schwarz 2002; Wood et al. 2020b; Dermane et al. 2021). In order to conserve this use, a neotype is designated below for *A. succinea*. As a result of these numerous changes, the updated statuses and synonymies are given here:

***Andrena* (*Pruinosandrena*) *parata* Warncke, 1967, stat. nov.**

Andrena pruinosa parata Warncke, 1967: 233, ♀♂ [Spain: OÖLM, examined].

Remarks. Though described from south-eastern Spain, Warncke (1976) noted that he had examined a single specimen of *A. parata* (as *A. pruinosa parata*) from Madrid: Ribas de Jarama, but he expressed doubts as to whether or not it had been correctly labelled given the collecting localities of all other known specimens. The contemporary Camino de Uclés site is approximately 7 km from Ribas de Jarama, confirming the presence of this taxon in central Spain.

Distribution. Spain.

Material examined. Spain: Alicante [38.3628°N, -0.5093°W], 1♂, leg. G. Mercet, OÖLM (holotype); Benidorm, 2.vi.1952, 1♀, leg. J. de Beaumont, OÖLM (paratype); Fortuna [Murcia], v.1928, 1♂, leg. J. M. Dusmet y Alonso, OÖLM (paratype); Madrid, Rivas-Vaciamadrid, Canal de Manzanares to Camino de Uclés, 19.v.2021, 1♀, leg. T.J. Wood, TJWC [BOLD accession number WPATW192-21].

***Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835**

Andrena pruinosa Erichson, 1835: 104, ♀ [Spain: ZMHB, examined].
Andrena lanuginosa Spinola, 1843: 137, ♀ [Spain, lectotype by present designation: MRSN].

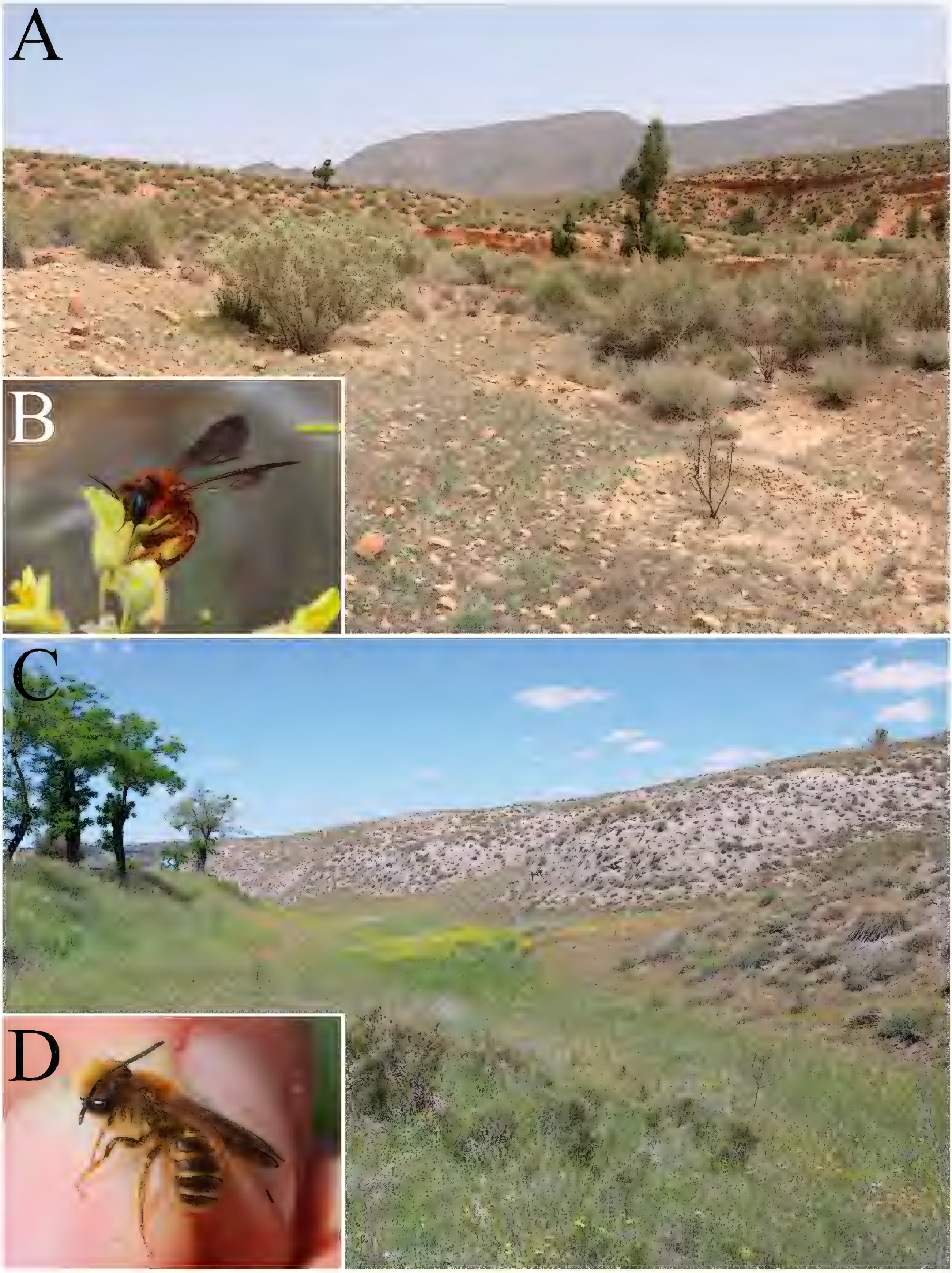

Figure 34. *Andrena* (*Pruinosandrena*) *succinea* Dours, 1872 **A** habitat, Oriental, Guercif, P5427, 2 km SW of Bou Rached, 950 m, 13.v.2022 **B** female collecting pollen from Brassicaceae spp.; *Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835 **C** habitat, Madrid, Chinchón, 6 km N, M-311, 14.v.2021 **D** male, in hand.

Remarks. Examination of the type material of both *A. pruinosa* and *A. lanuginosa* (Fig. 36) showed that both were female specimens with dark terga, conforming to the classical concept of this species. Neither represent *A. parata*, and hence the synonymy of *A. lanuginosa* with *A. pruinosa* is maintained. Spinola (1843) did not specify how many specimens he described the species from. The specimen examined here may be automatically the holotype, but as this is not clear from the original description, it is here designated as the lectotype.

Distribution. Spain.

Material examined. Spain: Andalusia, 1♀, leg. Waltl, ZMHB (holotype/syntype; Fig. 33); Andalusia, 1♀, leg. Ghilinni, MRSN (lectotype of *A. lanuginosa*, by present designation; Fig. 36); Madrid, Madrid, Chinchón, 6 km N, M-311, 14.v.2021, 2♂, 1♀, leg. T.J. Wood, TJWC; Madrid, Madrid, Pinto, 1 km E, Carr. la Marañosa, 13.v.2021, 1♂, 1♀, leg. T.J. Wood, TJWC.

Andrena (*Pruinosandrena*) *succinea* Dours, 1872, stat. nov.

Andrena succinea Dours, 1872: 424, ♀ [Algeria: type lost, neotype designated below, OÖLM].

Andrena chrysopyga Dours, 1872: 423, ♀ (nec. *Andrena chrysopyga* Schenck, 1853) [Algeria: type lost].

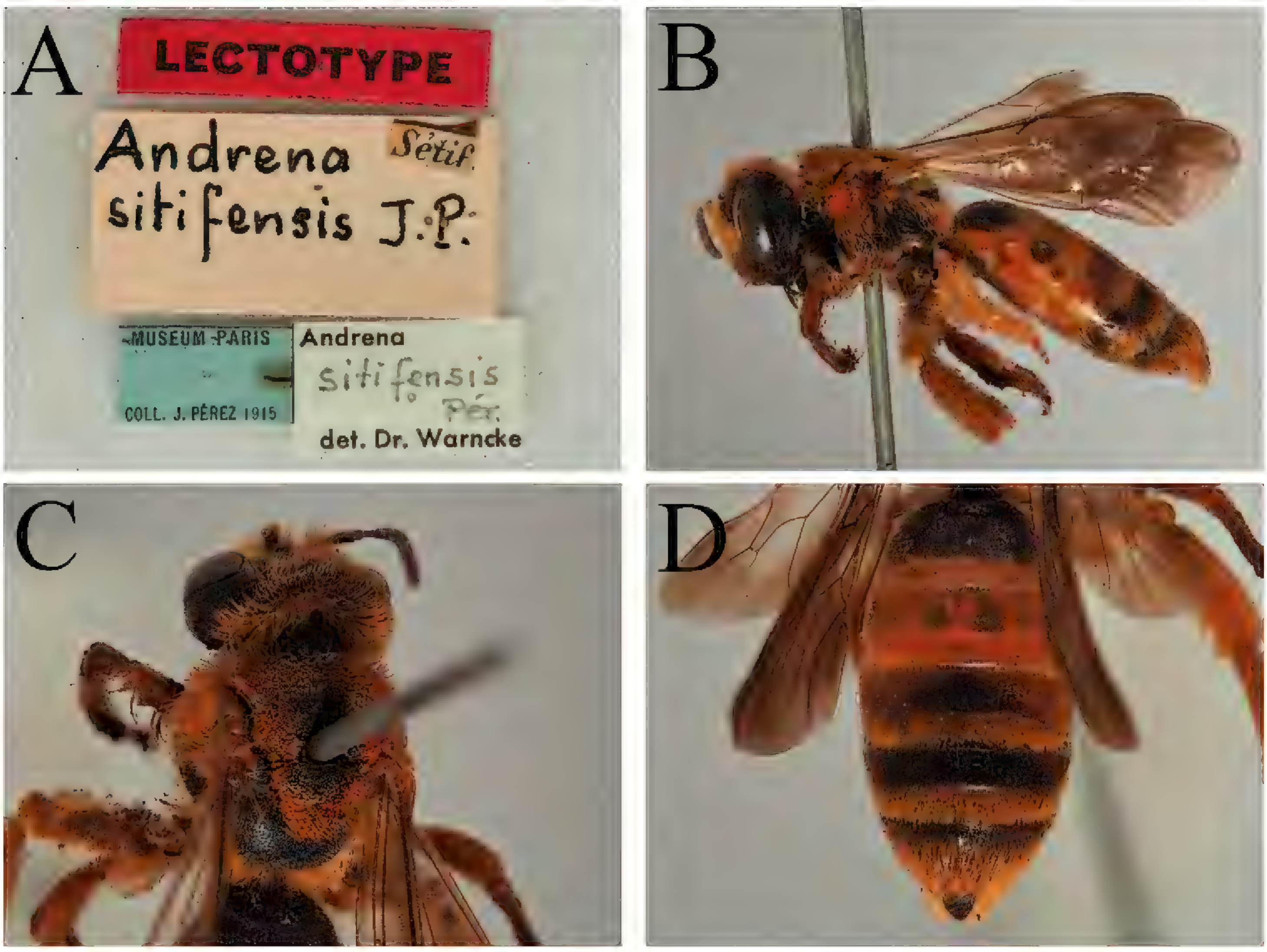

Figure 35. *Andrena* (*Pruinosandrena*) *sitifensis* Pérez, 1895, female lectotype **A** label details **B** profile **C** scutum, dorsal view **D** terga, dorsal view.

Andrena commixta Dalla Torre & Friese, 1895: 43. nom. nov. for *Andrena chrysopyga* Dours, 1872
Andrena sitifensis Pérez, 1895: 46, ♀ [Algeria: MNHN, examined]
Andrena fulvisquama Popov, 1940: 260, ♀ [Algeria: ZISP, not examined]

Remarks. The synonymy of *A. mayeti* Pérez, 1895 (described from Tunisia) with *A. succinea* reported by Warncke (1967, see also Benoist 1961) is incorrect. Examination of the female lectotype (Fig. 37) shows that *A. mayeti* syn. nov. is a synonym of *A. caroli* Pérez, 1895 (described from Algeria; Fig. 38) because the foveae are wide and there are well-developed hair bands on the tergal margins (see identification key for *Pruinosandrena* below).

Distribution. Morocco, Algeria, Tunisia, Libya, Egypt, Israel and the West Bank, Jordan, Syria, Saudi Arabia, Iran (Wood and Monfared 2022).

Material examined. Algeria: Setif [36.2059°N, 5.3965°E], 1♀, MNHN (lectotype of *A. sitifensis*; Fig. 35); Morocco: Oriental, Guercif, P5427, 2 km SW of Bou Rached, 33.8844°N, -3.6154°W, 950 m, 13.v.2022, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW389-22] (neotype of *A. succinea*, see below).

Figure 36. *Andrena* (*Pruinosandrena*) *lanuginosa* Spinola, 1843, female lectotype **A** label details **B** profile **C** head, dorso-frontal view **D** terga, dorsal view.

Figure 37. *Andrena* (*Pruinosandrena*) *mayeti* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

Andrena (*Pruinosandrena*) *caroli* Pérez, 1895

Andrena (*Pruinosandrena*) *caroli* Pérez, 1895: 47, ♀ [Algeria: MNHN, examined]
Andrena (*Pruinosandrena*) *mayeti* Pérez, 1895: 47, ♀ [Tunisia: MNHN, examined] syn. nov.

Distribution. Morocco, Algeria, Tunisia, Egypt, Israel.

Material examined. Algeria: Biskra [34.8600°N, 5.6995°E], 1♀, MNHN (lectotype of *A. caroli*; Fig. 38); Tunisia: Chott el Djerid [33.8806°N, 8.1435°E], 1♀, MNHN (lectotype of *A. mayeti*; Fig. 37).

The *numida*-group

This group of Palaearctic species was previously placed in the subgenus *Thysandrena* Lanham, 1949 by Warncke (1968a). However, true *Thysandrena* occur only in North America, and Palaearctic species fall elsewhere (Pisanty et al. 2022b). Four species are recognised in the Palaearctic; *A. hypopolia* Schmiedeknecht, 1884, *A. numida*, *A. ranunculorum* Morawitz, 1877, and *A. lunata* Warncke, 1975, though additional

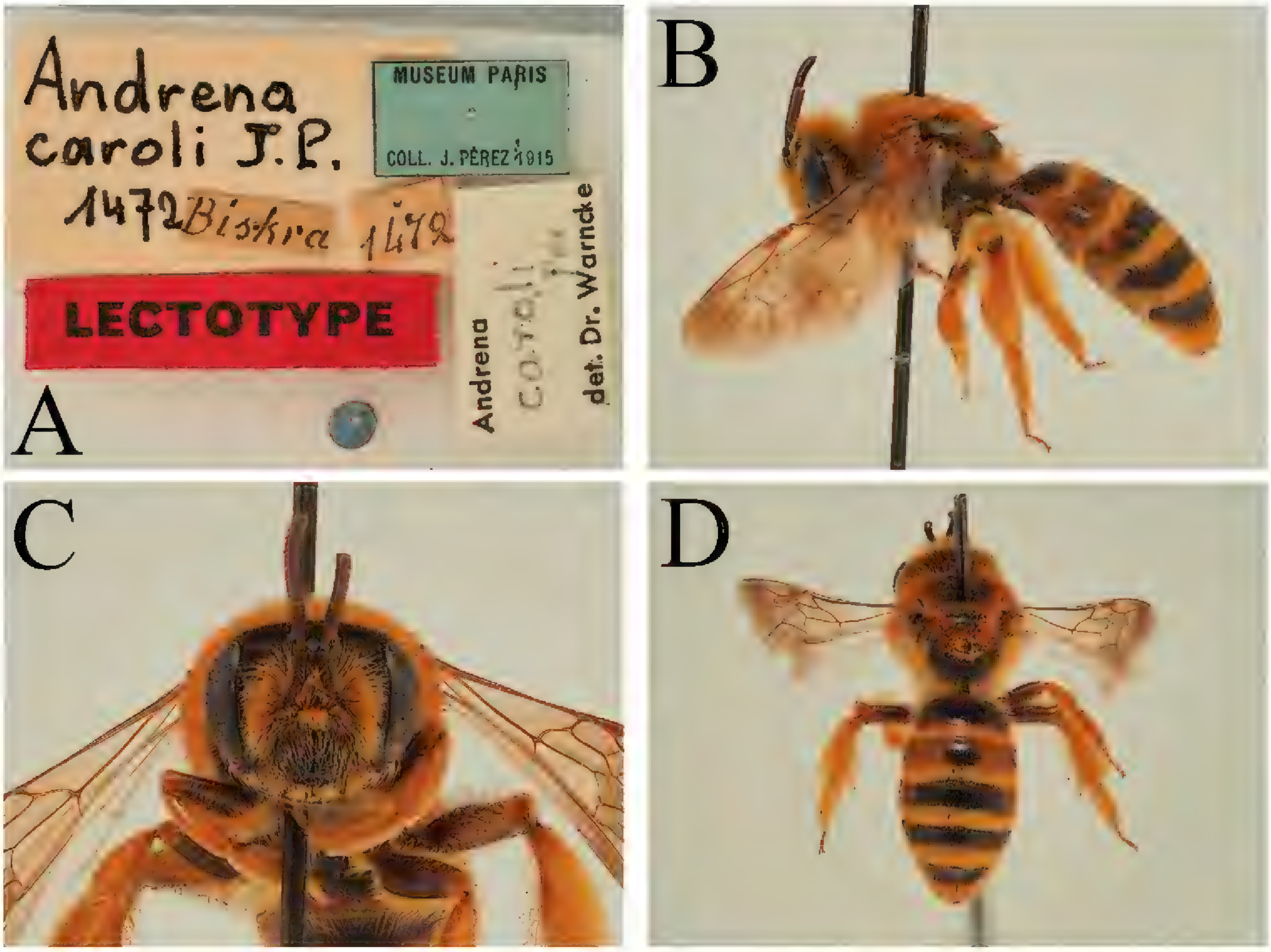

Figure 38. *Andrena* (*Pruinosandrena*) *caroli* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

genetic work is required to ensure that they all belong together; no subgenus is therefore described in the current work.

The status of *A. hypopolia* (described from southern France) has been somewhat unclear, as no major morphological differences from *A. numida* (described from Algeria) are apparent. Warncke used *A. hypopolia* in combination with *A. numida* as the subspecies for south-western Europe, using several other taxa as subspecies for populations in Central and Eastern Europe (ssp. ?*holosericea* Bramson, 1879, considered a *nomen dubium* by Gusenleitner and Schwarz 2002), southern Italy (ssp. *syracusae* Strand, 1921), and Turkey (ssp. *albiscopa* Warncke, 1967, see Gusenleitner and Schwarz 2002). No members of this group are known from the Levant.

The situation is further complicated because the type of *A. hypopolia* is lost (and could not be found amongst undesignated Schmiedeknecht type material located in the RMNH collection, see below), and the type of *A. numida* can also not be located at the MNHN. Furthermore, *A. inconspicua* Morawitz, 1871 was described from Calabria in southern Italy. Warncke (1967) treated this as *A.* (*Taeniandrena*) *russula* Lepeletier, 1841 based on the description; Gusenleitner and Schwarz (2001) then listed it as a synonym of *A. numida*, before finally Gusenleitner and Schwarz (2002) listed it as a synonym of *A. hypopolia* despite the fact that it is an older name. This is because,

under the broad treatment of Warncke, *A. inconspicua* would be junior to *A. numida*. However, Gusenleitner and Schwarz (2002) treated *A. hypopolia* as a distinct species, and did not resolve the status of *A. inconspicua*, even though it is an older name than *A. hypopolia*. The lectotype of *A. inconspicua* was recently illustrated by Astafurova et al. (2021), confirming its affinity with the *numida*-group, and not the subgenus *Taeniandrena*. The use of the name *A. inconspicua* therefore depends on two things; 1) whether European and North African material are distinct, and 2) whether material from southern Italy shows a stronger affinity with the European or North African taxon.

Genetically, barcoded specimens from Iberia showed almost no differentiation from specimens from Germany (average genetic distance 0.26%; Fig. 1), thus demonstrating that the name *A. hypopolia* can be applied to both the south-western and Central European populations. However, there was a consistent separation between Moroccan and German/Iberian sequences, these separated by an average genetic distance of 3.05% (range 2.87–3.13%). A single sequence was available from Sicily. This sequence differed from German/Iberian sequences by an average genetic distance of 6.11% (range 3.87–6.82%) and from Moroccan sequences by an average of 2.39% (range 2.17–2.64%). It clustered with Moroccan sequences, with the clades Morocco+Sicily showing bootstrap support of 92 and Germany+Iberia showing bootstrap support of 86. Examination of these barcoded specimens shows that there is a subtle but consistent morphological difference, which is the density of punctures on T3 of females. In Iberian specimens, the disc of T3 is densely punctate, with punctures separated by <1 puncture diameter. In contrast, in Moroccan and Sicilian specimens, the disc of T3 is shallowly and obscurely punctate, with punctures separated by >1 puncture diameter. Examination of the female lectotype of *A. inconspicua* (Astafurova et al. 2021: fig. 24) shows that this specimen morphologically conforms to *A. numida*, with weak and obscure punctures on the disc of T3. On this basis, *A. inconspicua* is synonymised syn. nov. with *A. numida*, and *A. hypopolia* is maintained as the senior name for populations in Iberia and Central Europe. A barcoded neotype of *A. numida* is designated from Moroccan material (see below).

This action largely maintains the *status quo* of Gusenleitner and Schwarz (2002), and *A. numida* is considered to have a distribution of Morocco, Algeria, Tunisia, Libya, and Sicily and the extreme southern parts of Italy (Calabria, Campania). The inclusion of Campania derives from treatment of the taxon *A. syracusae*. This taxon was described by Strand in the male sex only as a variety of *A.* (*Simandrena*) *propinqua* Schenck, 1853. Warncke (1967) treated this as a subspecies of *A. numida* with dark facial hair. The barcoded specimen from Sicily is a female, and whilst it should represent *A. syracusae* since it was collected only 150 km west of the *locus typicus* of Syracuse, since the female of *A. syracusae* is unknown and undescribed this cannot be said for certain. I have not seen male *A. numida* material from Sicily, or the type material of *A. syracusae* itself. However, I have seen males from the island of Ischia by Naples. These conform to the concept of *A. syracusae*, with extensive dark facial pubescence, and show extremely weak and sparse punctation on T3. The island of Ischia and the nearby Sorrento Peninsula on the Italian mainland are unusual and host an *Andrena* fauna with

several species that are otherwise found in Italy only in Sicily, such as *A.* (*Micrandrena*) *fumida* Pérez, 1895. On the basis of its morphology, *A. syracusae* is considered to represent only a form of *A. numida*. This should ultimately be confirmed through the direct barcoding of males with dark facial pubescence; these are expected to fall into the *A. numida* clade.

The status of *A. numida albiscopa* is unclear, but based on its distribution and morphology (T3 is clearly punctured), it is transferred to *A. hypopolia albiscopa* comb. nov. The punctures of T3 are sparser than in *A. hypopolia* s. str., and the interspaces are shinier. This is true also of *A. hypopolia* material from Central Asia (Kyrgyzstan). For now, a conservative position is taken that *A. hypopolia* ranges from Iberia to Central Asia and western Siberia, though the eastern limit and the status of material from Turkey requires validation through genetic analysis across this range.

Finally, examination of the lectotype of *A. setosa* Pérez, 1903 (Fig. 39; des. Warncke 1967) reveals that it is not a synonym of *A. numida hypopolia* as given by Warncke (1967), but a synonym (syn. nov.) of *Andrena ranunculorum*. The specimen comes from Arreau in France which is in the Hautes-Pyrénées department, and is situated immediately adjacent to mountains that ascend to 3,000 m. *Andrena ranunculorum* is known from alpine habitats in the central and eastern Pyrenees on both the French and Spanish sides, so this synonymy makes both morphological and ecological sense.

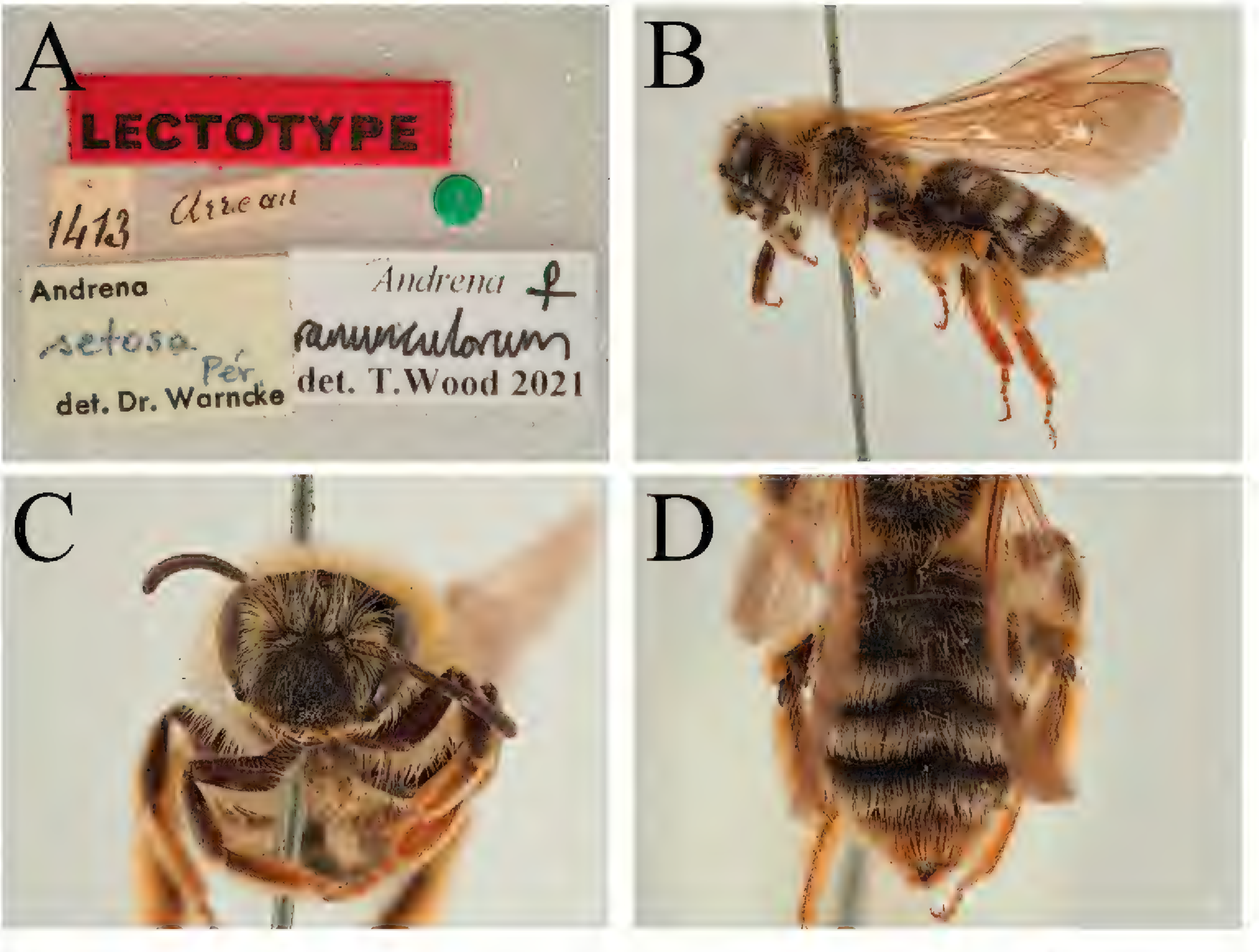

Figure 39. *Andrena* (incertae sedis) *setosa* Pérez, 1903, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

Material examined. ***Andrena ranunculorum*:** **France:** Arreau [42.9064°N, 0.3557°E], 1♀, MNHN (lectotype; Fig. 39).

***Andrena numida* f. *syracusae*:** **Italy:** Campania, Is. Iscia, Panza, 9.iv.1991, 6♂, leg. J. Gusenleitner, OÖLM/TJWC.

***Andrena fumida*:** **Italy:** Kampanien, Salerno, Monti Alburini (NP), SE Petina, 1100 m, 8.vi.2003, 1♀, leg. H. & R. Rausch, OÖLM; Mondello [Palermo, Sicily], 10.iv.1979, 1♂, leg. J.A.W. Lucas, OÖLM; Monte Faito (Campania), 13.v.1976, 1♂, leg. Pagliano, MRSN; Sorrento [Naples], 3.v.1970, 1♂, leg. J.P. van Lith, RMNH.

Description of new subgenera

Subgenus *Blandandrena* subgen. nov.

https://zoobank.org/E78F170A-60CC-4D38-9D56-9727B1347DDC

Type species. *Andrena blanda* Pérez, 1895.

Diagnosis. *Blandandrena* is monotypic, and hence diagnosis of *A. blanda* (Fig. 40) is *de facto* diagnosis of the subgenus. Through the combination of slightly upturned fore margin of the clypeus, fovea broad and occupying over ½ the space between the lateral ocellus and the inner margin of the compound eye, weak but distinct humeral angle, unmodified posterior face of the hind femur (without teeth, carinae, or spines), lack of squamous hairs, simple hind tibial spur (not broadened basally or medially), dark integument, black male clypeus, and essential absence of defining features it falls very close to members of the *relata*-group and to *Ovandrena* subgen. nov. that were formerly lumped together under the subgenus *Poliandrena* (see above). *Andrena blanda* females can provisionally be separated from the *relata*-group by the weakly punctate terga, punctures shallow and somewhat obscure, separated by 1–2 puncture diameters (Fig. 40D) whereas in the *relata*-group, tergal punctures are typically much stronger, clear and dense, separated by 1–2 puncture diameters but often by only 1 puncture diameter. This character works for West Mediterranean members of the *relata*-group, but additional work is needed to define this subgenus in the east, and so it is not defined and described here. *Andrena blanda* females can be separated from the *Ovandrena* by their simple scutal hairs (Fig. 40A–C; hairs semi-squamous in *Ovandrena*) and poorly delineated propodeal triangle that lacks lateral carinae (Fig. 40C; propodeal triangle clearly defined by presence of lateral carinae in *Ovandrena*; see below for additional detail).

Andrena blanda males can be separated by their black clypeus (Fig. 40F) in combination with their distinctive genital capsule (Fig. 40G). Most members of the *relata*-group have a yellow-marked clypeus, but for those with a black clypeus (e.g. *A. corax*), the genital capsule allows recognition. In *A. blanda*, the genital capsule is short and compact, more or less round, with gonocoxae with apically diverging inner margins and which are produced into short pointed teeth, and the gonostyli are apically strongly broadened and flattened, the disc being slightly broader than long. In the *relata*-group, the genital capsule is typically simple, without strongly apically broadened gonostyli, or when this is the case (e.g. *A. murana* Warncke, 1975a) then the clypeus is yellow-marked and the

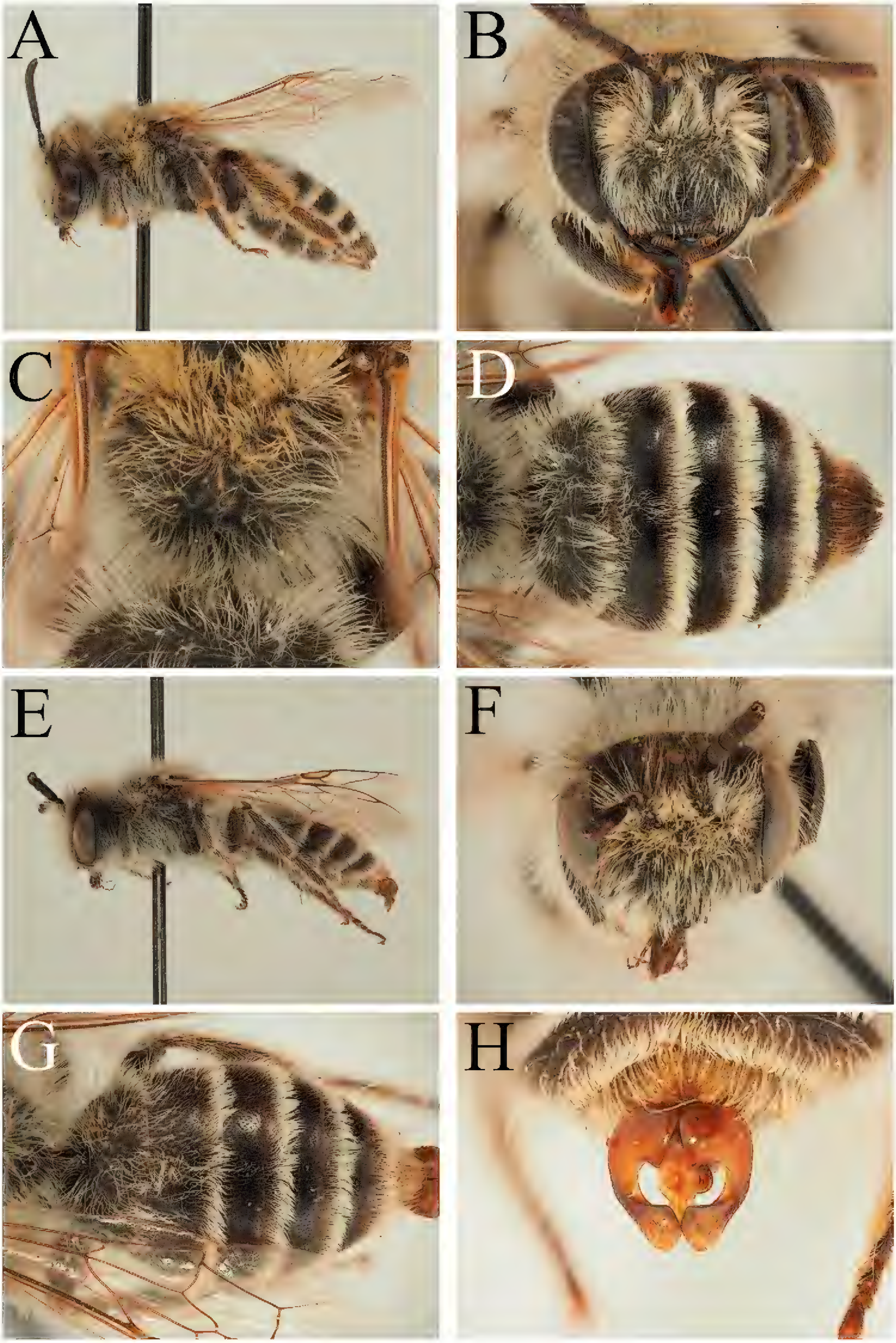

Figure 40. *Andrena* (*Blandandrena*) *blanda* Pérez, 1895, female **A** profile **B** face, frontal view **C** propodeum, dorsal view **D** terga, dorsal view; male **E** profile **F** face, frontal view **G** terga, dorsal view **H** genital capsule.

gonocoxae are not produced into pointed teeth. *Andrena blanda* can be separated from the *Ovandrena* by the genital capsule, as in *Ovandrena* the gonostyli are apically flattened and spatulate, but the disc is always longer than broad. The gonocoxae are also produced into apically projecting teeth, but the inner margins of the gonocoxae are parallel and do not diverge. The propodeal triangle of *Ovandrena* is also triangular and strongly defined by lateral carinae, whereas in *A. blanda* it is poorly defined and lacks lateral carinae.

Description. Medium-sized bees (9–10 mm) with dark integument. Head broad, 1.4 times broader than long. Gena slightly exceeding width of compound eye; ocelloccipital distance 1.5–2 times diameter of lateral ocellus, slightly broader in male sex. Facial fovea broad, occupying almost entire distance between lateral ocellus and inner margin of compound eye. Mesosoma dorsally with moderately long light brown hairs, laterally with white hairs. Pronotum laterally with humeral angle. Dorsolateral surface of propodeum with obscure and finely raised rugosity; propodeal triangle broad, poorly delineated laterally, surface with fine granular reticulation, basally with weakly raised rugosity, propodeal triangle thus defined by change in surface sculpture. Forewing with nervulus antefurcal. Hind tibial spurs simple, not broadened basally or medially. Terga weakly and obscurely punctate, punctures separated by 1–2 puncture diameters. Male genital capsule rounded, more or less circular in outline, gonocoxae with inner margins apically diverging, produced into apically projecting short pointed teeth. Gonostyli apically broadened and flattened, apical disc slightly broader than long. Penis valves relatively narrow, occupying less than half space between gonostyli.

Etymology. The name is taken from the name of the type species *A. blanda*, with *blanda* being the feminine singular of the adjective *blandus* which can mean pleasant, agreeable, smooth. It can be used to refer to the generally unremarkable nature of the species which has made it hard to assign to a particular group of species. The gender is feminine.

Included species. *Andrena blanda* (Spain, including mainland Spain and newly recorded for Fuerteventura), Morocco, Algeria, Tunisia; Gusenleitner and Schwarz 2002).

Material examined (illustrative). Algeria: Biskra [34.8600°N, 5.6995°E], 1♀, MNHN (lectotype des. Warncke 1967); 5 km N of Mecheria, st. 9, 7.iv.1983, 1♀, leg. R. Leys & P. v. d. Hurk, RMNH; 5 km SE of Sfissifa, st. 8, 6.iv.1983, 1♀, leg. R. Leys & P. v. d. Hurk, RMNH; Morocco: Drâa-Tafilalet, Tazenakht, 1 km W Anezal, c. 1600 m, 15.iv.2022, 1♀, leg. T.J. Wood, TJWC; Foum Zguid, 50 km N, 30.iii.1986, 1♂, 16♀, leg. M. Schwarz, MSC; Ifkern, 25 km E Boulemane, 25.v.1995, 10♀, leg. Mi. Halada, OÖLM; Spain: Fuerteventura, Costa Calma, ESE Montaña Pelada, 29.iii.2015, 3♀, leg. A. Müller, AMC/TJWC; Fuerteventura, S Costa Calma, Montañeta de los Verdes, 1.iv.2015, 5♀, leg. A. Müller, AMC; Sierra de María, 25 km W Lorca, 10.v.2003, 1♀, leg. J. Halada, OÖLM; Granada, Pantano de los Bermejales, 26.v.1982, 1♀, leg. R. Leys, RMNH.

Subgenus *Bryandrena* subgen. nov.

https://zoobank.org/54B1C9C7-8D5A-441B-B49B-DDBA8FB5FE39

Type species. *Andrena florea* Fabricius, 1793.

Diagnosis. *Bryandrena* is monotypic, and hence diagnosis of *A. florea* is *de facto* diagnosis of the subgenus. The combination of broad head (Fig. 41B, F; 1.3–1.4 times broader than long), the inner margins of the compound eyes diverging ventrally, humeral angle (stronger in male), punctate clypeus with underlying surface shiny over the majority of its area, propodeal triangle not defined by lateral carinae and comparatively smooth relative to the microreticulate dorsolateral parts of the propodeum (Fig. 41C), terga that are always at least partially red-marked (Fig. 41D, G), unmodified posterior face of the hind femur (without teeth, carinae, or spines), lack of squamous hairs, simple hind tibial spur (not broadened basally or medially), black male clypeus, and unique genital capsule (Fig. 41H; see description below) allows separation from any other *Andrena* species.

Description. Medium-sized bees (11–13 mm), integument predominantly dark, with red markings on at least one tergum, sometimes all terga extensively red marked. Head broad, 1.3–1.4 times wider than long, inner margins of compound eyes diverging ventrally. Gena slightly exceeding width of compound eye in females, clearly exceeding width of compound eye in males; ocelloccipital distance 1.5–2 times diameter of lateral ocellus. Facial fovea broad, occupying ¾ of distance between lateral ocellus and inner margin of compound eye. Pronotum laterally with humeral angle, more pronounced in male sex. Dorsolateral surface of propodeum microreticulate, with weakly raised reticulation; propodeal triangle poorly defined laterally, comparatively smooth and lacking microreticulation, basally with raised rugosity covering variable extent, never entire propodeal triangle. Forewing with nervulus interstitial. Terga regularly and densely punctate, punctures separated by 1 puncture diameter. Male genital capsule strongly elongate, gonocoxae essentially truncate with inner margin rounded, gonostyli apically produced, elongate, strongly flattened and spatulate, 3 times longer than broad; penis valves basally broad, strongly narrowing medially to become elongate and acutely pointed apically.

Etymology. The name is taken from the pollen host plant *Bryonia* (Cucurbitaceae) which ultimately derives from the Greek βρυωνία [bruōnía]. *Andrena florea* can be found frequently almost wherever *Bryonia* species are in flower. The gender is feminine.

Included species. *Andrena florea* (West Palaearctic, from Morocco and Iberia to Iran and the Ural Mountains; Gusenleitner and Schwarz 2002).

Subgenus *Limbandrena* subgen. nov.

https://zoobank.org/E0948E05-DB8C-4AD2-B260-01D335F6EA96

Type species. *Andrena limbata* Eversmann, 1852 (illustrated by Astafurova et al. 2022).

Remarks. Historically, *A. toelgiana* Friese, 1921 has been considered the sister species to *A. limbata*, differing by the yellow clypeus in the female sex (see Gusenleitner and Schwarz 2002). However, the male is unknown. Structurally, there are no differences. Examination of specimens from Bulgaria and Turkey show a gradient of yellow colouration on the clypeus, from entirely black, with a narrow longitudinal yellow

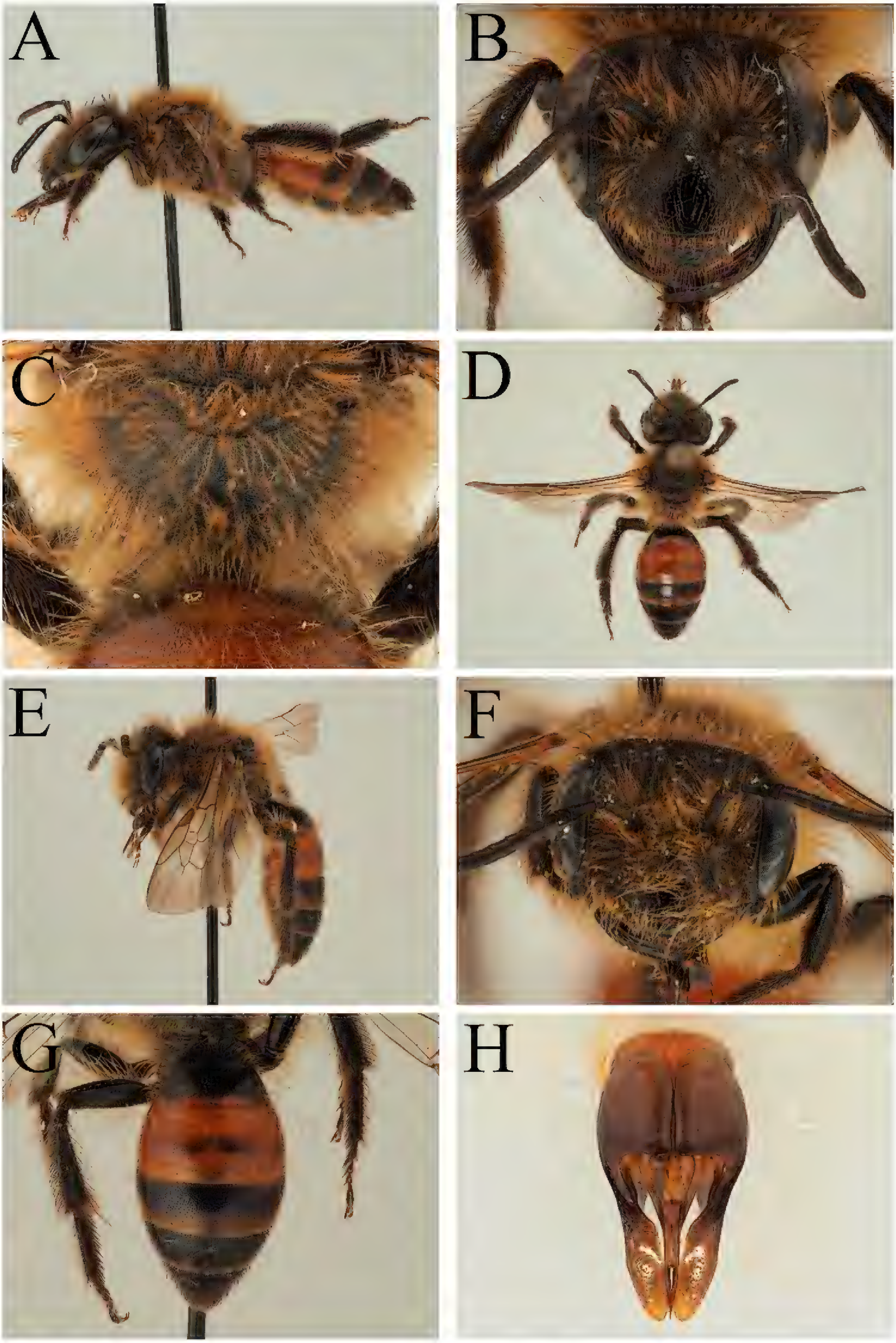

Figure 41. *Andrena* (*Bryandrena*) *florea* Fabricius, 1793, female **A** profile **B** head, frontal view **C** propodeum, dorsal view **D** dorsal view; male **E** profile **F** face, frontal view **G** terga, dorsal view **H** genital capsule.

strip, predominantly yellow-marked, and entirely yellow-marked (Fig. 42). Across this gradient there is also variation in the strength of the tergal hair bands, with material nominally conforming to *A. toelgiana* falling closer to *A. limbata* s. str. in displaying clear hair bands, whereas the subspecies *A. limbata dusmeti* Warncke, 1975 (Portugal, Spain, southern France, north-western Italy) has hair bands that are almost absent in fresh specimens (Figs 43C–H, 44A, B, E, F). On the basis of this colour gradient, absence of structural characters, and lack of a described male that could offer a distinctive difference, *A. toelgiana* syn. nov. is synonymised with *A. limbata*.

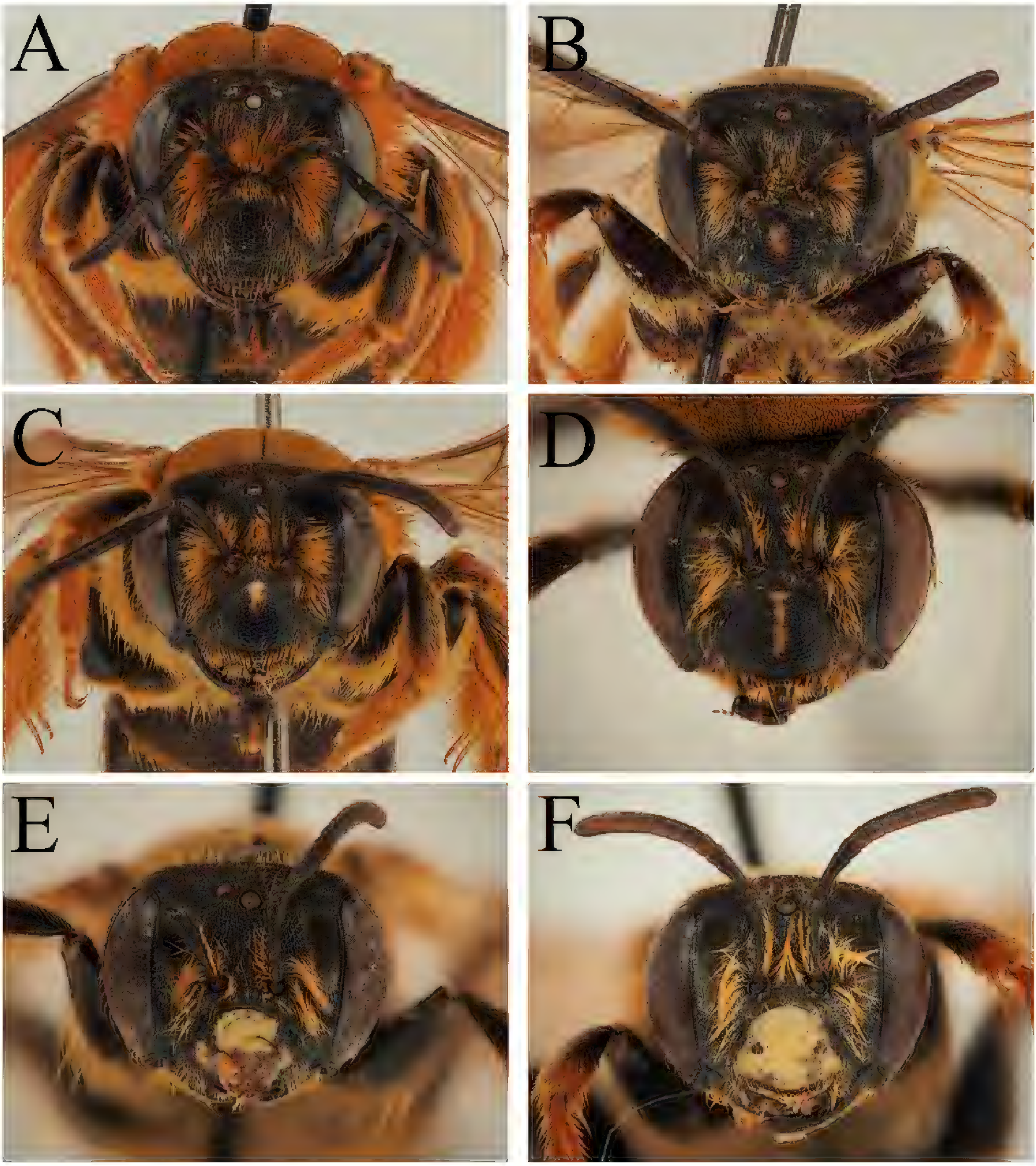

Figure 42. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852 female head in frontal view on west-east gradient **A** Spain **B** Bulgaria **C** Turkey (Gürün) **D** Turkey (Bingöl) **E** Turkey (Bingöl) **F** Turkey (Diyarbakır).

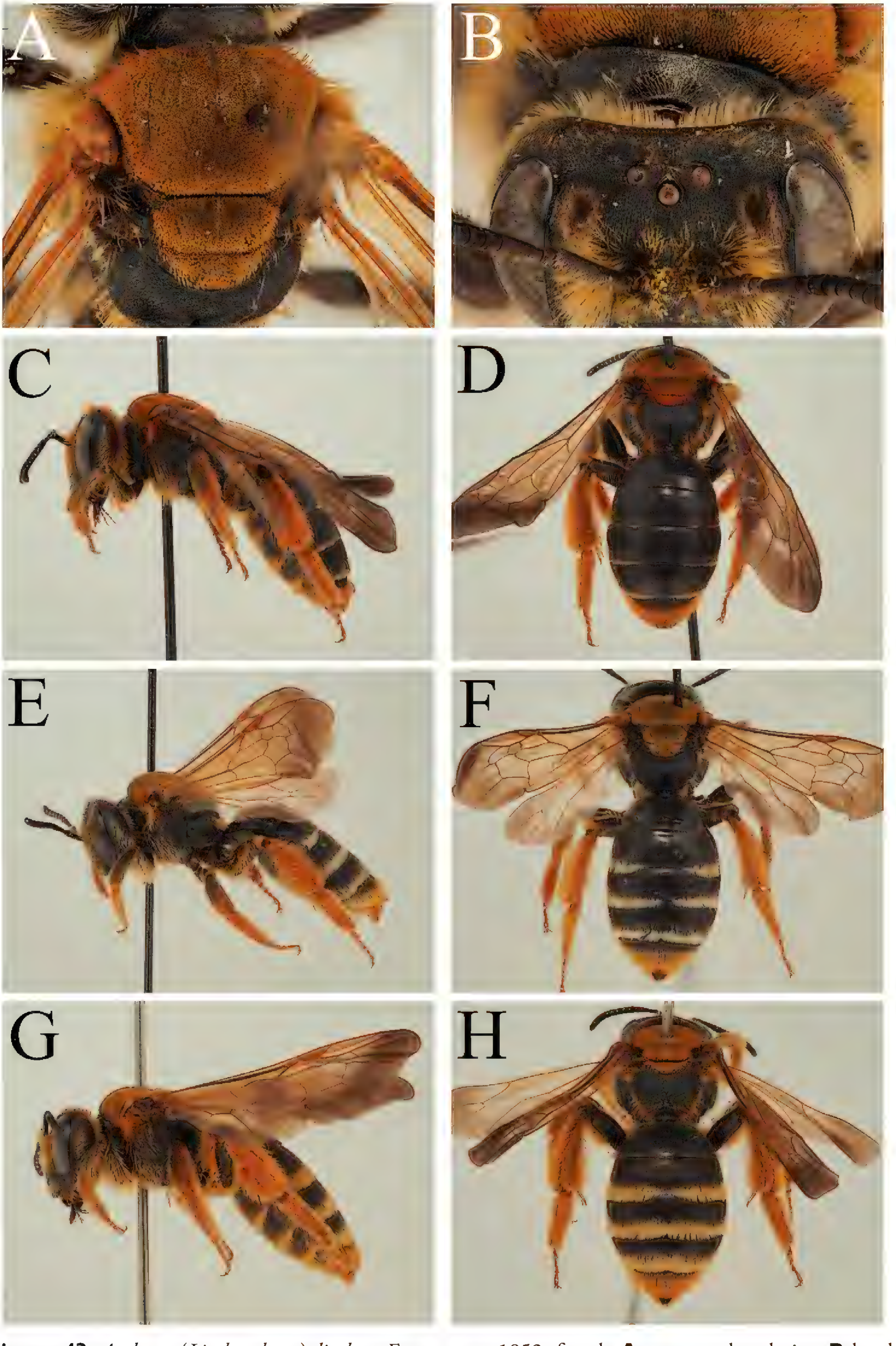

Figure 43. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852, female **A** scutum, dorsal view **B** head, dorso-frontal view; *Andrena limbata dusmeti* Warncke, 1967 female **C** profile **D** terga, dorsal view; *A. limbata* s. str. female, Bulgarian specimen **E** profile **F** terga, dorsal view; *A. limbata* s. str. female, Turkish specimen **G** profile **H** terga, dorsal view.

Diagnosis. *Limbandrena* (and, *de facto*, *A. limbata*) can be recognised in the female sex due to the combination of squamous brown hairs on the scutum, scutellum, and metanotum (Fig. 43A), the long ocelloccipital distance equal to three times the diameter of a lateral ocellus (Fig. 43B), the posterior face of the hind femur which lacks a transverse carina and transverse row of raised teeth or spines, the weakly and shallowly punctate dorsolateral surfaces of the propodeum, the laterally clearly delineated and internally finely rugose propodeal triangle (not rugosely areolate), the pronotum with at most a weak lateral angle, the more or less squarish head which is only 1.1 times wider than long, and the simple hind tibial spur that is not broadened basally or medially.

Males can be recognised by most of the same characters: the yellow clypeus (Fig. 44C, D), the relatively rounded head which is only 1.1–1.2 times broader than long (Fig. 44C, D), the long ocelloccipital distance equal to three times the diameter of a lateral ocellus, the pronotum with at most a weak lateral angle, the weakly and shallowly punctate dorsolateral surfaces of the propodeum, the laterally clearly delineated and internally finely rugose propodeal triangle (not rugosely areolate), and the genital capsule with weakly produced rounded gonocoxal teeth, gonostyli with weakly raised and rounded projection on inner margin, and penis valves with rounded lateral hyaline extensions (Fig. 44G, H). No other *Andrena* species shows this combination of characters.

Description. Medium-sized bees (11–14 mm) with dark integument with exception of yellow maculations on female (sometimes) and male clypeus (always). Head 1.1–1.2 times broader than long, compound eyes with inner margins weakly converging apically. Gena slightly exceeding width of compound eye; ocelloccipital distance long, 3 times diameter of lateral ocellus. Facial fovea moderate, occupying ½ space between lateral ocellus and compound eye. Female scutum, scutellum, and metanotum covered with short brown squamous hairs. Pronotum laterally with weak humeral angle. Dorsolateral surface of propodeum weakly and shallowly but regularly punctate, punctures separated by 0.5–1 puncture diameter. Propodeal triangle clearly delineated laterally by raised carinae, internal surface with clear pattern of fine rugosity medially, not extending over entire area. Forewing with nervulus strongly postfurcal. Hind tibial spurs simple, not broadened basally or medially, apically weakly bent. Terga densely and finely punctate, punctures separated by 0.5 puncture diameters. Male genital capsule slightly elongate, with produced and weakly rounded gonocoxal teeth. Gonostyli with weakly raised and rounded projection on inner margin. Penis valves produced into rounded hyaline extensions laterally, occupying majority of space between gonostyli.

Etymology. The name is taken from the name of the type species *A. limbata*, with *limbata* being the feminine singular of the adjective *limbatus* which means edged or fringed, probably in reference to the distinct squamous hairs on the female scutum and scutellum. The gender is feminine.

Included species. *Andrena limbata* (Europe from Portugal and Spain to Turkey, Israel, northern Iran, and the Ural Mountains; Gusenleitner and Schwarz 2002).

Material examined (illustrative). **Albania:** Lopan [Lapanj], 14.vi.2018, 2♀, leg. Kobe Janssen collection (Belgium); **Bulgaria:** Lozenec [Lozenets, Лозенец]/Mičurin, 24.vi.1988, 5♀, leg. B. & O. Tkalců, OÖLM; **Croatia:** Istrien, Rovinjsko Selo, 8–9.

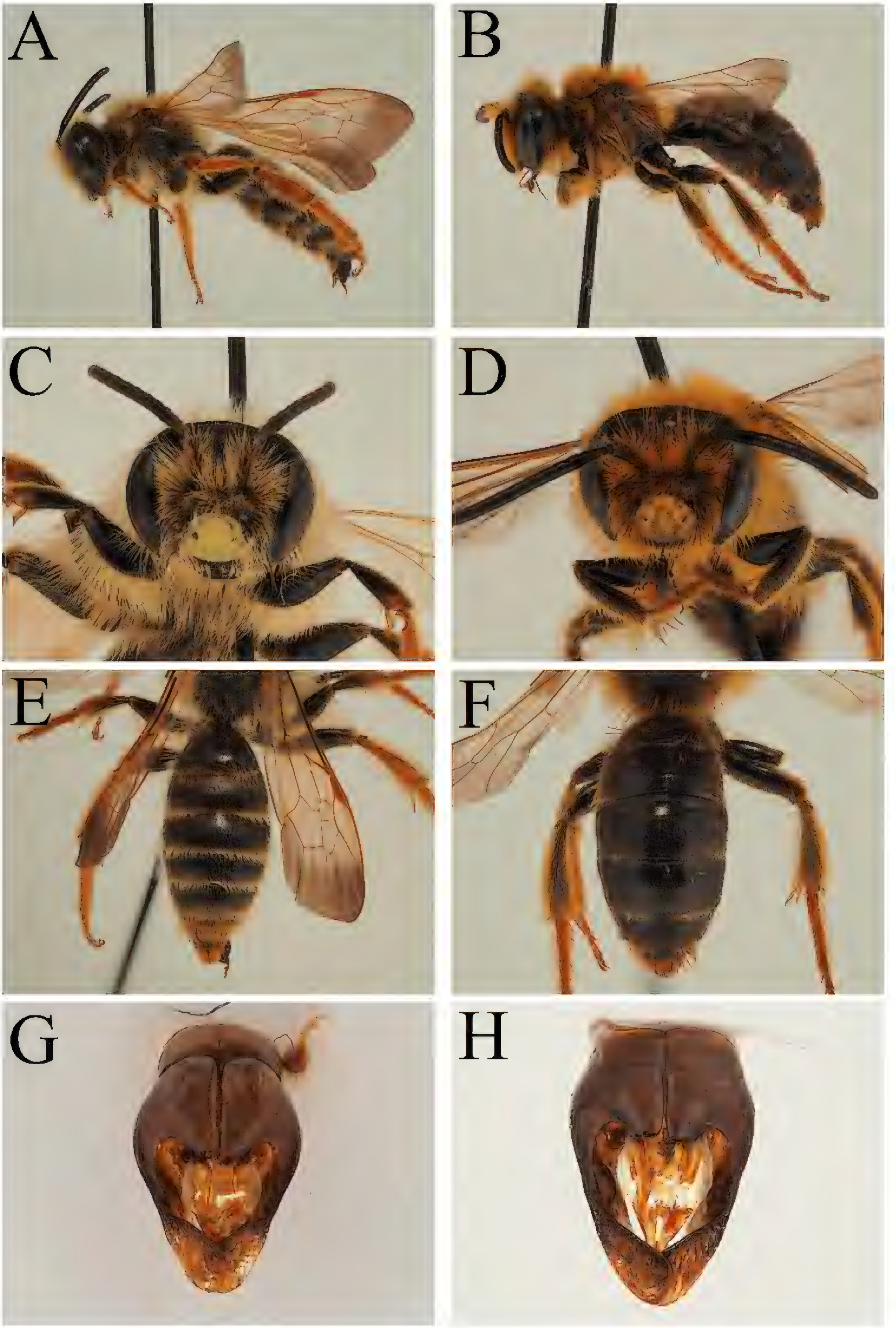

Figure 44. *Andrena* (*Limbandrena*) *limbata* Eversmann, 1852, Turkish male **A** profile **C** face, frontal view **E** terga, dorsal view **G** genital capsule; *Andrena limbata dusmeti* Warncke, 1967, Spanish male **B** profile **D** face, frontal view **F** terga, dorsal view **H** genital capsule.

vi.2012, 1♀, leg. Holzmann, OÖLM; **France:** B. d. R., Fontvieille, 28.v.1993, 4♀, leg. H. & J.E. Wiering, RMNH; **Georgia:** E Tbilisi, lori river S Sagarejo, 19.vi.2015, 3♀, leg. M. Snižek, OÖLM; **Greece:** Kos I. Kefalos, 4.v.1989, 2♀, leg. K.M. Guichard, NHMUK; Peloponnese, 12 km NWW Sparti, 26.v.2005, 1♀, leg. M. Kadlecová, OÖLM; **Italy:** Arezzo, Oliveto, 28.v.1989, 3♀, leg. H. & J.E. Wiering, RMNH; Piemonte, S. Benefetto Belbo, 10.vi.1979, 1♀, leg. Pagliano, MRSN; **Portugal:** Manteigas, Serra da Estrela [40.4009°N, -7.5396°E], 28.iv.–9.vii.1929, 1♀, leg. Kricheldorf, OÖLM (holotype of *A. limbata dusmeti*); **Spain:** Segovia, Madrona, 500 m NE, Arroyo del Hocino, 15.v.2021, 1♂, 2♀, leg. T.J. Wood, TJWC; Ávila, Hoyocasero, 1350 m, 20.v.1995, 1♂, 2♀, leg. H. & J.E. Wiering, RMNH; **Turkey:** Tanin-Tanin-Pass, 1700 m, 12.vi.1984, 1♀, OÖLM; Karatepe/Adana, 17.iv.1984, 3♂, 1♀, leg. K. Warncke, OÖLM; Akyaka, Yeşilova, 20.vi.2016, 1♀, leg. M. Kasparek, OÖLM.

Subgenus *Ovandrena* subgen. nov.

https://zoobank.org/A122C278-C33D-4790-A34A-FC270AE6A962

Type species. *Andrena oviventris* Pérez, 1895.

Diagnosis. Through the combination of slightly upturned fore margin of the clypeus, broad fovea occupying at least ½ the space between the lateral ocellus and the inner margin of the compound eye, weak but distinct humeral angle, unmodified posterior face of the hind femur (without teeth, carinae, or spines), simple hind tibial spur (not broadened basally or medially), dark integument, black male clypeus, and essential absence of defining features it falls very close to members of the *relata*-group and to *Blandandrena* that were formerly lumped together under the subgenus *Poliandrena* (see above).

In the female sex, *Ovandrena* species differ from these groups by only a single major character: the structure of the propodeal triangle (Fig. 45A, B). *Ovandrena* species have scutal hairs that are not as short and clearly squamous as in members of the *Aenandrena*, *Limbandrena*, or *Lepidandrena* Hedicke, 1933, but they are partially squamous in some species (Fig. 45C, D), whereas the scutal hairs in the *relata*-group and *Blandandrena* are typically simple, though in some species such as *A. corax* the hairs can be semi-squamous. The structure of the propodeal triangle is therefore the only character that allows consistent separation. In *Ovandrena*, the propodeal triangle is a broad and well-defined triangle (lateral margins extending almost to the lateral edges of the metanotum) that is defined by raised carinae; the internal surface is covered in raised irregular carinae of a similar width, therefore appearing homogenous and consistent (Fig. 45A, B). In the *relata*-group and *Blandandrena*, the propodeal triangle varies from smooth and undefined to weakly defined with at most irregular rugosity on its internal surface, but never approaches the condition in *Ovandrena*. The combination of these two characters therefore always allows recognition. They can also be partially recognised by the extremely dense and fine punctation of the terga, punctures separated by <0.5 puncture diameters; in comparison groups, the punctures are never this fine or this dense.

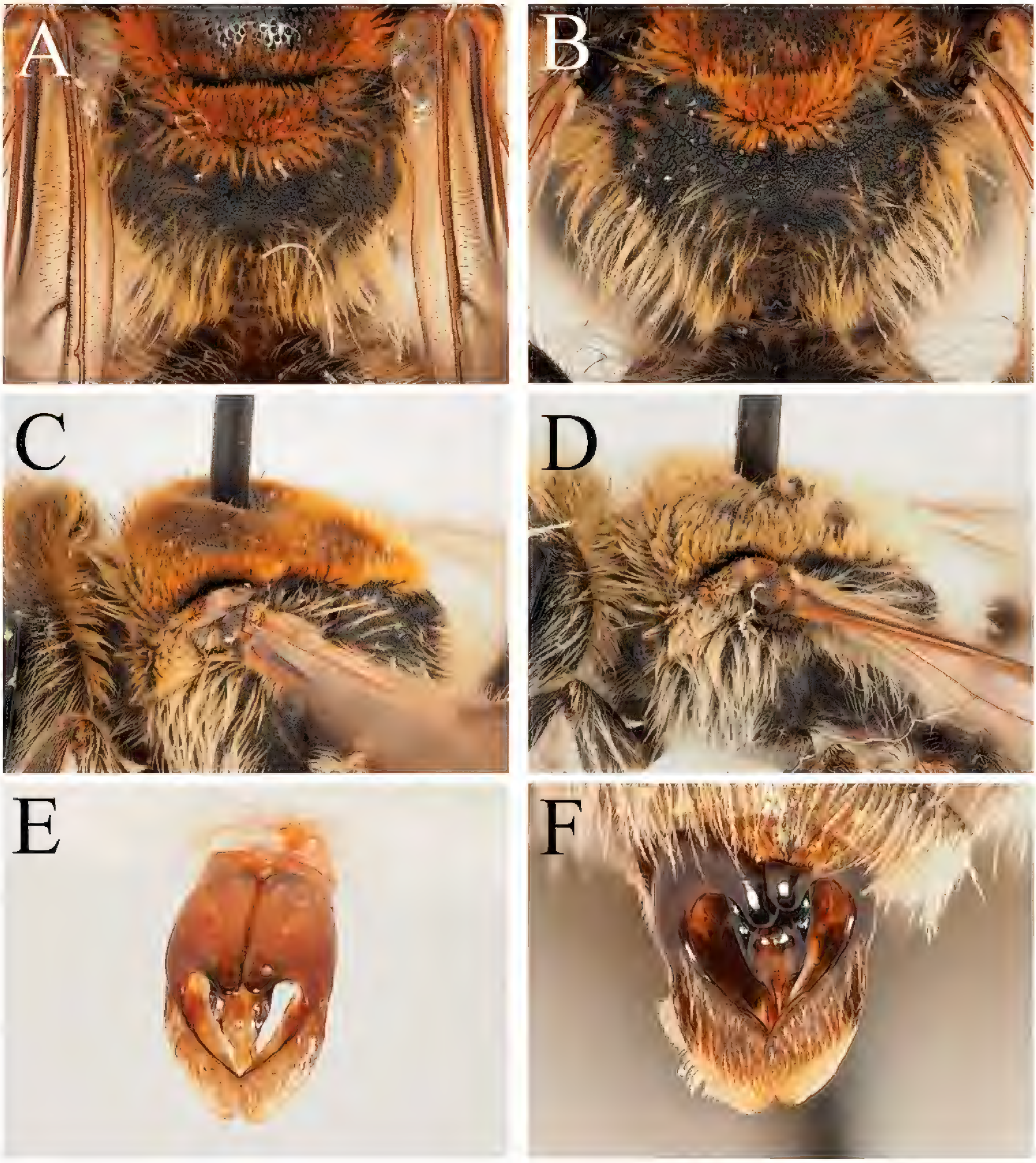

Figure 45. *Andrena* (*Ovandrena*) subgen. nov. characters. *Andrena* (*Ovandrena*) *marsae* Schmiedeknecht, 1900, female **A** propodeal triangle; *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895 **B** female propodeal triangle **C** female scutal hairs, profile view **F** male genital capsule; *Andrena* (*Ovandrena*) *farinosa* Pérez, 1895 **D** female scutal hairs, profile view **E** male genital capsule.

Males can be recognised through their combination of dark clypeus with upturned fore margin, distinctive propodeal triangle as in the female sex, pronotum with weak or strong humeral angle, A3 exceeding A4 but shorter than A4+5, and genital capsule which is compact with pronounced and rounded gonocoxal teeth (Fig. 45E, F). Members of the *relata*-group often have a yellow-marked clypeus, but for species showing a dark clypeus (e.g. *A. corax*), the clearly defined triangular propodeal triangle allows separation (smooth to at most weakly defined in the *relata*-group). Separation

can be made from *Blandandrena* by the genital capsule and the propodeal triangle, as detailed in the diagnosis section for that subgenus.

Description. Small to moderately sized bees (7–11 mm) typically with dark integument, one species with red tergal markings; male clypeus always dark. Head broad, 1.3–1.4 times broader than long, compound eyes with inner margins weakly converging apically. Gena slightly exceeding width of compound eye; ocelloccipital distance short, slightly less than to slightly more than diameter of lateral ocellus. Facial fovea moderately broad, occupying ½ distance between lateral ocellus and compound eye. Female scutum, scutellum, and metanotum covered with shortish light brown to whitish semi-squamous hairs (Fig. 45C, D). Pronotum laterally with weak to strong humeral angle. Dorsolateral surface of propodeum with regular and dense network of raised reticulation; propodeal triangle wide, lateral margins extending almost to lateral edges of metanotum, laterally defined by straight raised carinae, thus strongly triangular (Fig. 45A, B). Internal surface of propodeum covered by raised irregular carinae of a similar width, therefore homogenous and consistent. Forewing with nervulus interstitial to weakly antefurcal. Hind tibial spurs simple, not broadened basally or medially. Terga densely punctate, in females punctures extremely dense and fine, separated by <0.5 puncture diameters, in males punctures slightly sparser and coarser, separated by 0.5–1 puncture diameters. Male genital capsule compact, consistent across species, with gonocoxae strongly produced into apical rounded teeth (Fig. 45E, F). Gonostyli apically spatulate, with a more or less strongly raised inner margin. Penis valves basally narrow or moderately broad, in both cases becoming narrow medially.

Etymology. The name is taken from the type species for the genus, *A. oviventris*. It derives from the Latin *ovum* meaning egg, in reference to the egg-shaped metasoma. The gender is feminine.

Included species. *Andrena farinosa* Pérez, 1895 (Spain and France), *Andrena farinosoides* Wood, 2020 (Morocco), *Andrena marsae* Schmiedeknecht, 1900 (Morocco, Algeria, Tunisia), and *Andrena oviventris* (Morocco, Algeria, Portugal, Spain, France). The subgenus is therefore currently restricted to the Western Mediterranean, and the centre of diversity is Morocco. The status of *A.* (incertae sedis) *inusitata* Pisanty, 2022 must be resolved through genetic analysis (see Pisanty et al. 2022a).

Material examined. ***Andrena oviventris*: Algeria:** Teniet el Had [35.8727°N, 2.0007°E], 1♀, MNHN (lectotype; Fig. 46).

***Andrena farinosa*: Spain:** Murcie [Murcia], 1♀, MNHN (lectotype).

Identification key to subgenus *Ovandrena* subgen. nov.

1	Females	**2**
–	Males[1]	**5**

1 Note, males of these four species are extremely similar, and great care must be taken when separating them. Association with females should be made, as well as reference to their known biogeographical distributions and to confidently determined reference material.

2 Terga almost entirely red-marked, with at most slight black marks basally on T1 and two black spots laterally on T2 (north-western Africa) .... ***marsae*** **Schmiedeknecht**

– Terga dark, without red markings **3**

3 Scutum less densely punctate, punctures separated by at least 1 puncture diameter, surface clearly smooth and shiny between punctures (Morocco) .. .. ***farinosoides*** **Wood**

– Scutum densely punctate, punctures separated by 0.5 puncture diameters to confluent, narrow interspaces shiny **4**

4 Tergal discs glabrous, with hairs restricted to marginal areas. Larger, 10–11 mm (north-western Africa and south-western Europe).................. ***oviventris*** **Pérez**

– Tergal discs extensively covered with extremely short hairs, forming a velvety pubescence in addition to denser and longer hairs on tergal margins. Smaller, 8–9 mm (Spain and France only) .... ***farinosa*** **Pérez**

5 Larger, 9–10 mm. Tongue with outer surface of galea clearly punctate, punctures separated by 1–2 puncture diameters. Sterna with weak and sparse fringes on apical margins. Tergal punctation comparatively larger and coarser (north-western Africa and south-western Europe) .... ***oviventris*** **Pérez**

– Smaller, 7–8 mm. Tongue with outer surface of galea more or less smooth and shiny, without obvious punctures. Sterna with strong and dense fringes on apical margins. Tergal punctation comparatively fine **6**

6 Clypeus comparatively less densely punctate, punctures separated by 0.5–1 puncture diameters, with shiny interspaces, thus appearing shiny. Pronotum with humeral angle comparatively strong (Spain and France only) .... ***farinosa*** **Pérez**

– Clypeus comparatively more densely punctate, punctures separated by 0.5 puncture diameters, interspaces dull, thus appearing dull (north-western Africa) **7**

7 Viewed laterally and ventrally, tergal margins, ventrolateral parts of terga, and sternal margins usually lightened reddish orange-brown (north-western Africa)[2] .... ***marsae***

– Tergal and sternal margins dark to hyaline, never extensively lightened reddish orange-brown (Morocco only)[2] .... ***farinosoides***

Subgenus *Pruinosandrena* subgen. nov.
https://zoobank.org/62A1E8AF-01AD-4D69-8CD5-E20843A286D5

Type species. *Andrena pruinosa* Erichson, 1835.

2 These two species are almost identical in the male sex, and no structural characters are currently apparent.

Figure 46. *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895, female lectotype **A** label details **B** profile **C** face, frontal view **D** terga, dorsal view.

Diagnosis. This group of species was formerly placed in the subgenus *Campylogaster* due to the unusual character of the strongly and densely punctate mesepisternum and dorsolateral parts of the propodeum (punctures separated by <0.5 puncture diameters). However, as discussed above, *Campylogaster* sensu Warncke is polyphyletic and can be broken into three distinct clades (*Campylogaster* s. str., *Pruinosandrena*, and the *incisa*-group). All three share the distinctly punctate mesepisternum and also an extremely long ocelloccipital distance exceeding three times the diameter of the lateral ocellus. However, separation is straightforward. The true *Campylogaster* have the marginal area of the terga clearly and distinctly impressed with the apical margin reflexed; the impression therefore forms a latitudinal depressed furrow. In *Pruinosandrena*, the marginal areas of the terga are flat, without any kind of depression. In the *incisa*-group, the tergal margins are flat and the mesepisternum is densely punctate, but the dorsolateral parts of the propodeum have only raised reticulation, without punctures. The propodeal triangle is also clearly delineated by raised lateral carinae, whereas these are absent in *Pruinosandrena*. The combination of extremely long ocelloccipital distance, dense punctures on the mesepisternum and dorsolateral parts of the propodeum, and flat tergal marginal areas is therefore unique and characterises *Pruinosandrena*.

Description. Medium-sized bees (10–14 mm). Integument variable, from dark with at most tergal margins lightened hyaline-yellow to entirety of metasoma and legs red-marked; male clypeus yellow-marked in one species. Head moderately broad, 1.2 times broader than long. Gena broad, exceeding width of compound eye; ocelloccipital distance extremely long, at least 3 times diameter of lateral ocellus. Facial fovea variable, from narrow to occupying entirety of distance between lateral ocellus and inner margin of compound eye. Female scutum, scutellum, and metanotum with pubescence variable, in some species with extremely short squamous hairs, hairs longer and non-squamous in other species. Pronotum laterally with humeral angle. Mesepisternum and dorsolateral parts of propodeum densely and clearly punctate, punctures confluent to separated by <0.5 puncture diameters. Propodeal triangle without lateral carinae, internal surface with dense network of irregularly raised rugosity, thus contrasting punctate dorsolateral surface. Forewing with nervulus interstitial. Hind tibial spurs simple, not broadened basally or medially. Terga typically densely and finely punctate, punctures separated by 1 puncture diameter, at least on T2–5. Male genital capsule simple, compact, with gonocoxae apically truncate to produced into weak rounded teeth. Gonostyli apically spatulate, penis valves more or less narrow, parallel-sided, occupying less than ½ space between gonostyli.

Etymology. The name is taken from the type species for the subgenus, *A. pruinosa*. The Latin word *pruinosa* is the feminine singular of *pruinosus* which means 'frosty', in reference to the squamous hairs of the mesosoma. The gender is feminine.

Included species. *Andrena caroli* (Morocco to Israel); *Andrena nilotica* Warncke, 1967 (Spain); *Andrena parata* (Spain); *Andrena pruinosa* (Spain); *Andrena sparsipunctata* Wood, 2020 (Morocco); *Andrena succinea* (Morocco to Iran and Saudi Arabia). The centre of diversity is therefore Spain + Morocco, with all six species occurring here.

Identification key to subgenus *Pruinosandrena* subgen. nov.

Note, the male of *A. sparsipunctata* is unknown. The males described by Wood et al. (2020b) are actually misidentified *A. mediovittata* Pérez, 1895; *A. sparsipunctata* is expected to be restricted to south-western Morocco. See Wood et al. (2020b) for additional useful images.

1	Females **2**
–	Males **7**
2	In dorsal view, fovea broad, clearly occupying more than half of the distance between the lateral ocellus and the compound eye (Fig. 37C). Terga with strong apical pale hair bands that uniformly cover the entirety of the tergal depressions and obscure the underlying surface (Figs 37D, 38D; North Africa to Israel) .... ***caroli* Pérez**
–	Fovea narrow, occupying at most half the distance between the lateral ocellus and the compound eye (Figs 33B, 36C). Terga with or without clear hair

bands; if with hair bands, then hair bands typically do not uniformly cover the tergal depressions, either weaker basally or stronger apically **3**

3 T1 with extremely sparse punctures, punctures separated by 2–4 puncture diameters. Facial fovea along its entire length separated from the inner margin of the compound eye by a distance equal to its own diameter (south-western Morocco only) .... ***sparsipunctata* Wood**

– T1 with dense punctures, punctures separated at most by 2 puncture diameters, usually by 1 puncture diameter (Fig. 59D). Fovea not strongly separated from the inner margin of the compound eye.................................. **4**

4 Pubescence of scutum weakly squamous, anterior dorsolateral corners of scutum with pubescence longer, clearly exceeding width of antennae in length. Terga always predominantly red. Terga with clear apical hair bands. Punctation of T1 slightly spaced, punctures separated by 1–2 puncture diameters (eastern and south-eastern Spain only) .... ***nilotica* Warncke**

– Pubescence of scutum strongly squamous and short, anterior dorsolateral corners of scutum with pubescence short, clearly shorter than width of antennae (Figs 33C, 59C). Terga variable, red to black or any intermediate combination. Terga with or without clear apical hair bands. Punctation of T1 denser, punctures separated at most by 1 puncture diameter **5**

5 A3 exceeding A4+5 in length. Terga always extensively red-marked (central and south-eastern Spain)... ***parata* Warncke**

– A3 equalling A4+5 in length. Terga variable, from almost entirely black to entirely red-marked... **6**

6 Terga usually predominantly dark (Figs 33D, 36D). Found in Spain .... ***pruinosa* Erichson**

– Terga always extensively or entirely red-marked (Figs 35D, 59D). Found outside of Spain .... ***succinea* Dours**

7 Clypeus at least partly yellow-marked (North Africa to the Middle East).... .... ***succinea* Dours**

– Clypeus uniformly dark **8**

8 A3 very short, shorter than A4 (North Africa to Israel) .... ***caroli* Pérez**

– A3 at least slightly longer than A4... **9**

9 A3 exceeding A4+5 in length (central and south-eastern Spain) .... ***parata* Warncke**

– A3 not exceeding A4+5 .... **10**

10 Genital capsule without clear kink in the inner margins of the gonostyli (Fig. 85E). Scutum less densely punctate, punctures separated by 0.5 puncture diameters, with shiny interspaces, predominantly shiny (eastern and south-eastern Spain only)... ***nilotica* Warncke**

– Genital capsule with clear kink in the inner margins of the gonostyli (Fig. 85F). Scutum more densely punctate, punctures almost confluent, predominantly dull (central and southern Spain) ....***pruinosa* Erichson**

Description of new species

***Andrena* (*Avandrena*) *juliae* Wood, sp. nov.**

https://zoobank.org/C53C51E7-AA4A-43A1-85CC-6C4862ED1D19

Type material. ***Holotype.*** **Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 36.3273°N, -5.5986°W, 18.iii.2023, 1♀, leg. T.J. Wood, OÖLM.

Paratypes. **Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 1♀, leg. T.J. Wood, TJWC; Cádiz, Tarifa, 1 km N, grazing fields, 23.iii.2023, 1♀, leg. T.J. Wood, OÖLM.

Description. Female. Body length: 9 mm (Fig. 47A). ***Head*:** Dark, 1.4 times wider than long (Fig. 47B). Clypeus weakly domed, with fine granular shagreen, dull, overlain by weak raised rugosity, rugosity forming weak, obscure, and interrupted raised latitudinal striations; remaining surface impunctate. Process of labrum rounded rectangular, twice as broad as long, surface smooth and shiny. Gena equalling width of compound eye; ocelloccipital distance equals diameter of lateral ocellus. Foveae moderately broad, occupying half space between compound eye and lateral ocellus, short, ventrally extending to level of antennal insertions; foveae filled with black hairs (Fig. 47C). Face medially with light brown-white hairs covering clypeus and antennal insertions, intermixing with black hairs, becoming entirely black haired along inner margin of compound eyes and frons; gena and vertex with long light brown hairs, longest hairs equalling length of scape. Antennae dark, A7–12 ventrally slightly lightened grey by presence of scales; A3 equalling A4+5+6. ***Mesosoma*:** Scutum and scutellum with fine granular shagreen, very weakly shiny, predominantly dull, underlying surface shallowly and obscurely punctate, punctures separated by 1–2 puncture diameters (Fig. 47D). Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum with fine granular shagreen, predominantly dull, shagreenation overlain by fine network of raised rugosity, not forming a linked network. Propodeal triangle short and broad, slightly depressed below level of dorsolateral parts of propodeum, with extremely fine granular shagreen, basal 2/3rds covered with raised longitudinal rugae, propodeal triangle thus strongly contrasting dorsolateral parts of propodeum (Fig. 47E). Mesepisternum with long strongly plumose hairs, hairs predominantly pale with some intermixed black hairs, hairs clearly exceeding length of scape. Scutum and scutellum with strongly plumose light brown hairs, intermixed with black hairs medially. Propodeum with long strongly plumose light brown hairs, propodeal corbicula incomplete, dorsal fringe weak and poorly defined, internal surface with numerous pale simple hairs. Legs dark, tarsi obscurely lightened reddish brown; pubescence light brown. Flocculus complete, strong, composed of strongly plumose light brown hairs; femoral and tibial scopa composed of light brown simple hairs. Hind tibial claws with strong inner tooth. Wings hyaline, stigma and venation dark orange, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas narrowly lightened hyaline-yellow (Fig. 47F). Tergal discs with scattered and small hair-bearing punctures, punctures separated by 3–4 puncture diameters, underlying surface finely shagreened, silky smooth, shiny. Tergal discs with

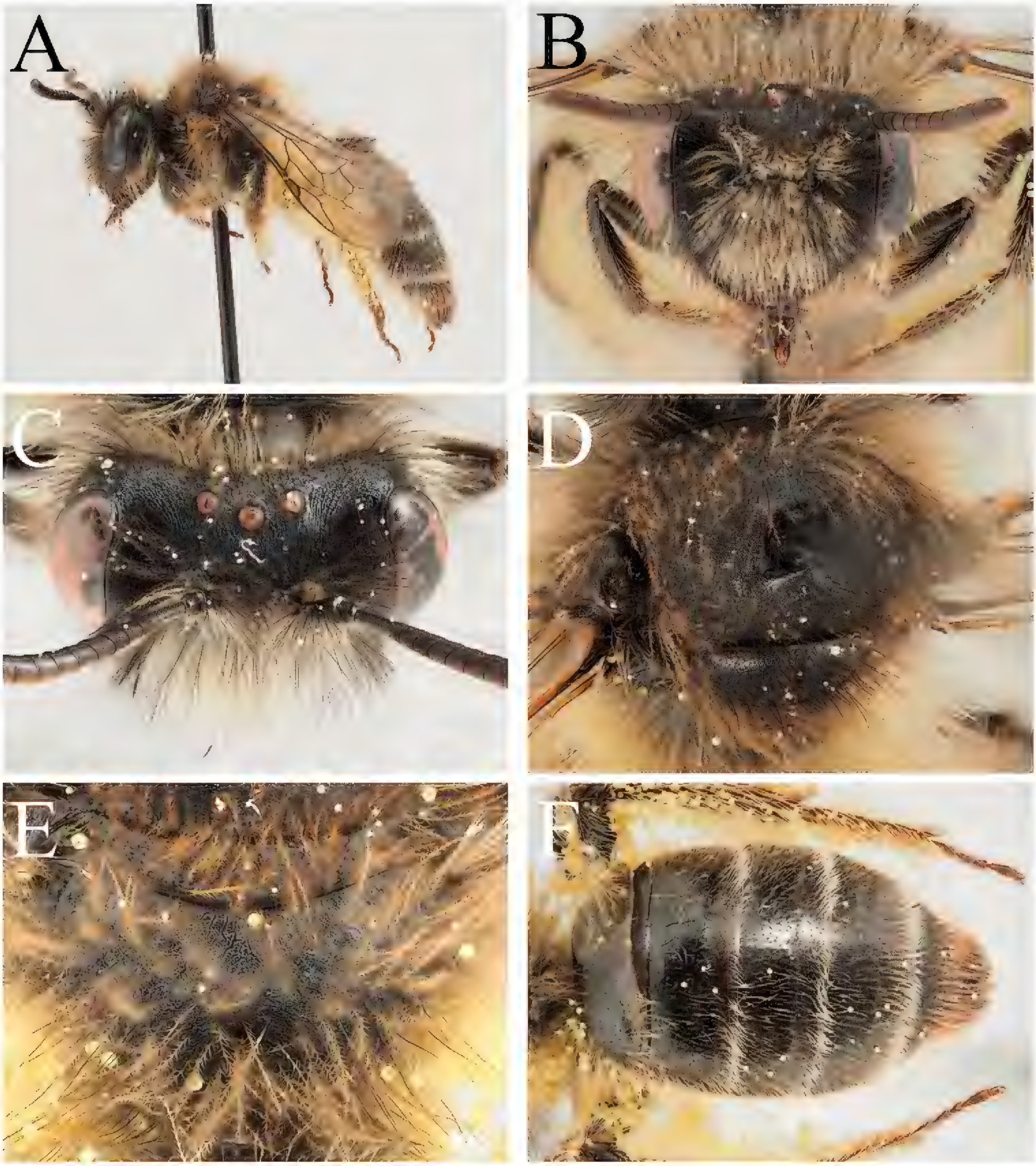

Figure 47. *Andrena* (*Avandrena*) *juliae* sp. nov. female **A** profile **B** face, frontal view **C** head, dorsal view **D** scutum, dorsal view **E** propodeum, dorsal view **F** terga, dorsal view.

sparse upstanding pale hair, T2–4 with dense apical whitish hair bands that obscure underlying surface. Apical fringe of T5 and hairs flanking pygidial plate dark brown; pygidial plate apically rounded, surface flat and featureless.

Male. Unknown.

Diagnosis. *Andrena juliae* can be recognised as belonging to the subgenus *Avandrena* due to its moderate to small body size (9 mm), short and wide head (clearly wider than long), and short and wide foveae that are only slightly longer than wide, as well as the behavioural observation that it is strongly associated with *Erodium* (Geranicaceae,

see Remarks). The posterior face of the hind femora lacks spines, separating the species from *A. avara* Warncke, 1967 and *A. panurgina* De Steffani, 1889 and placing it close to *A. melacana* Warncke, 1967 and *A. erodiorum* Wood & Ortiz-Sánchez, 2022.

Andrena juliae can be separated from both species by the structure of the propodeum which has the dorsolateral parts with fine granular shagreenation that is overlain by a fine network of raised rugosity, this rugosity not forming a linked network. The propodeal triangle itself is clearly differentiated, slightly depressed below the level of the surrounding parts of the propodeum and delineated by fine carinae, the surface with fine granular shagreenation and with a network of raised longitudinal carinae covering the basal 2/3rds. In contrast, *A. erodiorum* has the dorsolateral parts of the propodeum shiny, overlain with a fine network of raised rugosity that joins together to form a clear network (Fig. 73E). The propodeal triangle is clearly delinated by raised carinae and with the entire surface covered with longitudinal carinae. In *A. melacana*, the dorsolateral parts of the propodeum are entirely covered with fine granular shagreen, without an overlay of raised rugosity, with the propodeal triangle not depressed and with even finer granular shagreen, not strongly differentiated from the surrounding areas.

The propodeum of *A. juliae* therefore sits between both comparison species and is distinct from both. It can be further separated by the pubescence of the mesepisternum which is predominantly composed of pale hairs, with approximately 30% of these hairs black (in *A. melacana* with 50–60% of the hairs of the mesepisternum black; in *A. erodiorum* with only 10% of these hairs black), by the facial foveae which occupy half of the space between the compound eye and a lateral ocellus (occupying ¾ of this space in *A. erodiorum*), by the colour of the hairs of the apical fringe of T5 and those flanking the pygidial plate which are dark brown (golden-brown in *A. erodiorum*, dark brown in *A. melacana*), and by the pubescence of the terga which are covered in sparse erect white hairs, T2–4 with dense apical hair bands of white hairs that obscure the underlying surface (in *A. melacana* terga with sparse short pubescence, only forming weak apical tergal hair bands that do not obscure the underlying surface; pubescence very similar in *A. erodiorum*).

Remarks. All specimens were collected from *Erodium* spp. The two females from Las Algamitas were collecting pollen from this genus (*Erodium* pollen can be seen in Fig. 47A). Across sampling locations in Cádiz province during March 2023, four species of *Avandrena* were active, specifically *A. avara* sensu stricto, *A. juliae*, *A. melacana*, and *A. panurgina*. All species appear to be narrowly oligolectic on *Erodium* (see below), and *A. juliae* could be found in direct sympatry with *A. avara* sensu stricto, *A. melacana*, and *A. panurgina* at the Las Algamitas site and with *A. melacana* and *A. panurgina* at the Tarifa site. *Andrena erodiorum* is currently known only from south-eastern Spain (Albacete). One *A. juliae* female showed abraded body hairs, and no males were captured, implying that the flight season may begin in early March or even late February, perhaps offering a reason as to why this species has been overlooked until now.

Etymology. Dedicated to my friend and colleague Julia Jones (University College Dublin, Ireland) who invited me on the University field course during which this new species was discovered.

Distribution. Spain (Cádiz province).

Other material examined. ***Andrena avara*** **s. str.: Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 1♀, leg. T.J. Wood, TJWC; Cádiz, Bolonia, El Lentiscal, 24.iii.2023, 1♀, leg. T.J. Wood, TJWC.

Andrena melacana**: Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 3♂, 2♀, leg. T.J. Wood, TJWC; Cádiz, Tarifa, 1 km N, grazing fields, 19.iii.2023, 4♂, 6♀, leg. T.J. Wood, TJWC.

Andrena panurgina**: Spain:** Cádiz, Parque Natural Los Alcornocales, Las Algamitas, Finca Murtas, 18.iii.2023, 4♂, 3♀, leg. T.J. Wood, TJWC; Cádiz, Tarifa, 1 km N, grazing fields, 19–23.iii.2023, 6♂, 2♀, leg. T.J. Wood, TJWC.

Andrena **(*****Euandrena*****)** ***isolata*** **Wood, sp. nov.**

https://zoobank.org/08390D0E-AC36-4859-AE7E-BDD126D34BB8

Type material. ***Holotype*****. Spain:** Granada, Sierra Nevada, Trevélez to Refugio La Campiñuela, 37.0239°N, -3.2656°W, 1700–2400 m, 14.vi.2021, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW368-21].

Description. Female. Body length: 9.5 mm (Fig. 48A). ***Head*****:** Dark, 1.2 times wider than long (Fig. 48B). Clypeus weakly domed, densely and evenly punctate,

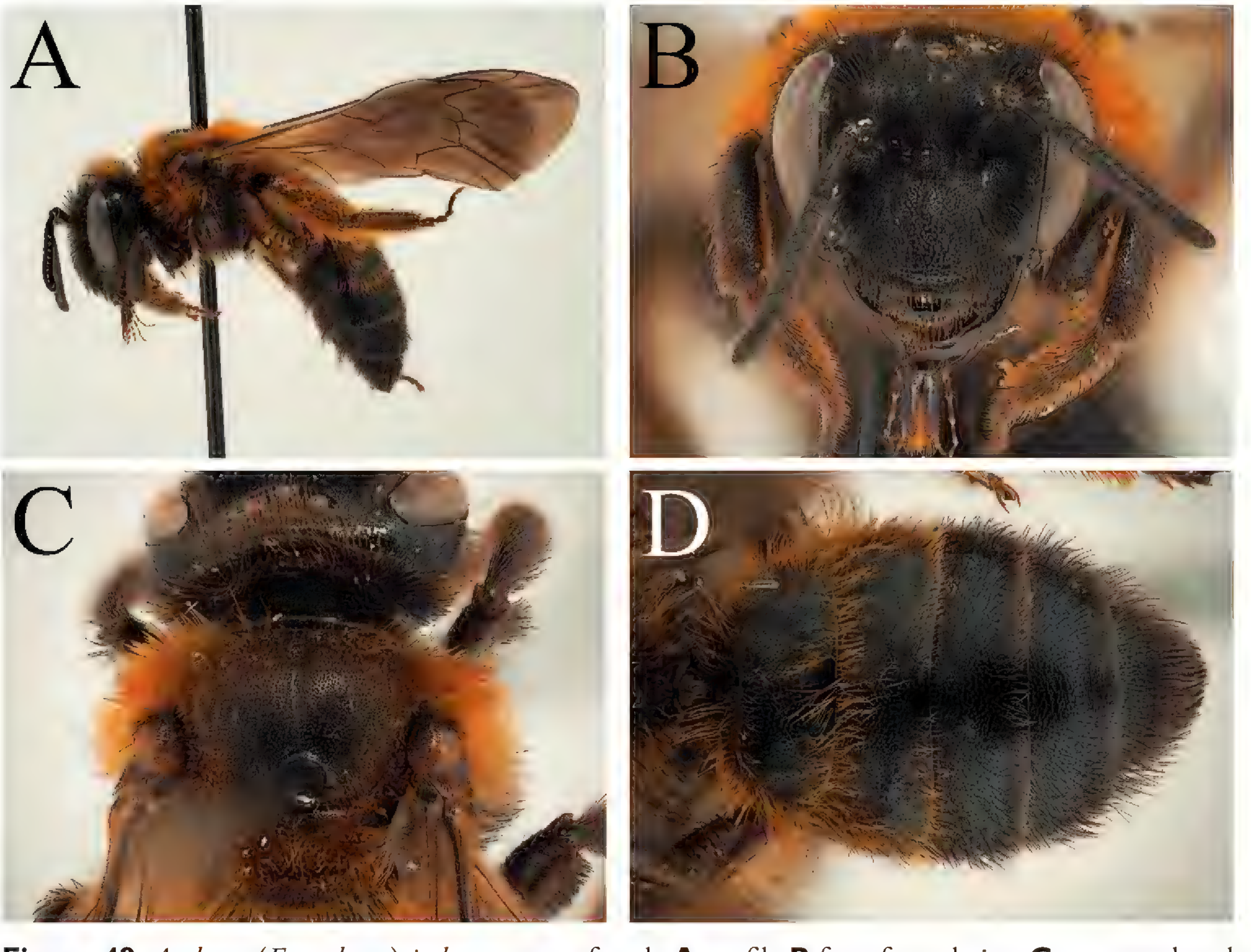

Figure 48. *Andrena* (*Euandrena*) *isolata* sp. nov. female **A** profile **B** face, frontal view **C** scutum, dorsal view **D** terga, dorsal view.

punctures separated by <0.5 puncture diameters, interspaces shiny. Process of labrum trapezoidal, twice as broad as long, apical margin with very weak emargination medially. Gena slightly exceeding width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus; vertex behind ocellar triangle densely punctate, punctures separated by 0.5 puncture diameters. Fovea dorsally narrow, occupying ⅓ of space between lateral ocellus and compound eye, ventrally reaching level of antennal insertions, here narrowing to ½ dorsal width; fovea filled with black hairs. Face, gena, and scape covered with uniformly short black hairs, vertex dorsally with predominantly golden-brown hairs with scattered intermixed black hairs. Antennae dark, A3 slightly exceeding A4+5, shorter than A4+5+6. ***Mesosoma*:** Scutum and scutellum densely punctate, punctures predominantly separated by <0.5 puncture diameters, at most by 1 puncture diameter medially, underlying surface finely shagreened and weakly shiny (Fig. 48C). Pronotum rounded. Mesepisternum microreticulate, weakly shiny to dull, with obscure raised reticulation. Dorsolateral parts of propodeum microreticulate, weakly shiny, densely and shallowly punctate, punctures separated by 0.5–1 puncture diameter. Propodeal triangle narrow, internal surface finely granulate and impunctate, basally with obscurely and weakly raised rugosity, propodeal triangle thus strongly contrasting punctate dorsolateral parts of propodeum. Mesepisternum ventrally with moderately long black hairs, becoming intermixed with golden-brown hairs medially, with entirely golden-brown hairs dorsally, hairs at most equalling length of scape. Scutum and scutellum dorsally with short golden-brown hairs, scutum medially with very short and obscure black hairs. Propodeum with long golden-brown hairs, propodeal corbicula incomplete, dorsal fringe composed of long plumose golden-brown hairs, internal surface with numerous plumose light hairs, becoming darker ventrally. Legs predominantly dark, hind femorae ventrally and posterior face of hind tibiae obscurely lightened reddish-orange; pubescence black to orange-brown. Flocculus incomplete, short, composed of weakly plumose orange hairs; femoral and tibial scopa orange, tibial scopa with at most occasional brown hairs dorso-basally. Hind tibial claws with strong inner tooth. Wings weakly infuscate, stigma and venation dark brown, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas very narrowly lightened hyaline-brown (Fig. 48D). Tergal discs regularly punctate, punctures separated by 1–2 puncture diameters, underlying surface shagreened, weakly shiny; punctures extending onto marginal areas, here weak and obscure, separated by 2–3 puncture diameters. T1–2 with orange-brown hairs basally, laterally, and apically; T2–3 with orange-brown hairs forming weak apical hair bands, not obscuring underlying surface, T4 with weak apical hair band black; discs of T3–4 with short black hairs. Apical fringe of T5 and hairs flanking pygidial plate black; pygidial plate rounded triangular, with slightly depressed and densely punctate area medially, lateral margins impunctate.

Male. Unknown.

Diagnosis. *Andrena isolata* can be quickly recognised as a *Euandrena* due to the narrow facial foveae (dorsally occupying ⅓ of space between the lateral ocellus and the compound eye) which narrow further ventrally combined with the long A3

(slightly exceeding length of A4+5) and the simple, non-plumose hairs of the tibial scopae. Its generally dark appearance with orange-brown hairs dorsally on the mesosoma and tibial scopa plus at least some black hairs on the mesepisternum place it immediately close to *A. bicolor* and allied taxa. As discussed above, the subgenus *Euandrena* is taxonomically complex, and multiple genetically distinct taxa have been lumped under *A. bicolor*. In an Iberian context, *A. isolata* is best diagnosed against *A. bicolor* s.l., *A. fortipunctata* Wood, 2021, and the distinct and probably undescribed taxon in north-western Africa identified above. Extreme care should be taken when identifying specimens morphologically, and barcodes should be used whenever possible.

In direct comparison to barcoded *A. bicolor* s.l. specimens, the only consistent character that can be identified is the structure of the clypeus. *Andrena isolata* has the clypeus densely punctate, with punctures separated by <0.5 puncture diameters, interspaces shiny but overall the clypeus only weakly shiny due to the small size of the interspaces (Fig. 48B). In *A. bicolor* s.l., the clypeal punctures are separated by an average of at least 1 puncture diameter, sometimes more, and the clypeus is therefore more strongly shiny due to the larger interspaces. The dense clypeal punctures place *A. isolata* close to *A. fortipunctata*, but the two species can be separated by the tergal structure (see illustrations in Wood et al. 2021), with the tergal margins weakly depressed with at most the apical rim lightened hyaline yellow (tergal margins strongly depressed and extensively lightened semi-translucent brown in *A. fortipunctata*), terga punctate with some punctures extending onto tergal margins, here separated by 2–3 puncture diameters (tergal margins impunctate in *A. fortipunctata*), margins of T2–3 with weak light brown hair fringes apically, T4 with entirely black hairs (T2–4 with white hair fringes emerging from junction between disc and margin, these hair fringes overlying marginal areas in *A. fortipunctata*), terminal fringe of T5 and hairs flanking pygidial plate black (terminal fringe and hairs flanking pygidial plate dark brown in *A. fortipunctata*). *Andrena isolata* is almost identical to the probably undescribed taxon from north-western Africa, but can also be separated by the structure of the clypeus. *Andrena isolata* has the clypeus densely punctate with punctures separated by <0.5 puncture diameters and with the interspaces shiny, whereas in the taxon from north-western Africa, the punctures are equally dense but the interspaces are shagreened and dull. Furthermore, this latter taxon has a short and shallow longitudinal furrow at the apex of the clypeus that is absent in *A. isolata*.

Remarks. *Andrena isolata* probably represents a relictual species that has become isolated on the Sierra Nevada from what is now a remaining North African population. Additional genetic sampling is needed to establish whether it is found away from the Sierra Nevada, but a specimen from the nearby Sierra de Baza collected at an altitude of 2000 m barcoded as *A. bicolor* s.l. [WPATW297-21]. *Andrena isolata* may well be restricted to the Sierra Nevada. Additional sampling is required to establish its ecology, including its voltinism. Its capture on *Campanula* implies that it has a similar ecology to *A. bicolor* s.l. (see Praz et al. 2019), but this requires dedicated study.

Etymology. Derived from the Latin *insulatus*, to be made into an island, *isolata* (feminine form) thus means to be isolated, in reference to its presence on the Sierra Nevada, separated from its nearest genetic relative in North Africa.

Distribution. Spain (Sierra Nevada).

Andrena (*Micrandrena*) *ortizi* Wood, sp. nov.

https://zoobank.org/F6956353-0278-4AE3-8C48-4084EDC29CCC

Type material. ***Holotype.*** **Spain:** Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 37.1239°N, -3.4322°W, 2100 m, 6.vi.2021, 1♀, leg. T.J. Wood, on *Vella spinosa* (Brassicaceae), OÖLM [BOLD accession number WPATW972-22].

Paratypes. **Spain:** Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 2100 m, 6.vi.2021, 2♀, leg. T.J. Wood, on *Vella spinosa* (Brassicaceae), OÖLM/TJWC; Granada, Sierra Nevada, Puerto de la Ragua, Barranco Maja Caco, 2000 m, 10.vi.2021, 1♀, leg. T.J. Wood, TJWC; Granada, Sierra Nevada 1900 m, ri. Veleta, 1.vi.1982, 1♀, leg. R. Leys, RMNH; Granada: Órgiva N, 1300 m, 26.vi.1988, 1♀, leg. M. Schwarz, OÖLM.

Description. Female. Body length: 7 mm (Fig. 49A). ***Head*:** Dark, 1.1 times wider than long (Fig. 49B). Clypeus long, apical margin clearly ventrally exceeding level of line between lower margins of compound eyes, surface weakly domed, irregularly punctate, punctures separated by 1–3 puncture diameters, impunctate longitudinal midline present; underlying surface basally finely shagreened and weakly shiny, shagreenation becoming weaker apically, here almost smooth and shiny. Process of labrum narrowly trapezoidal, slightly broader than long, apical margin narrowly truncate. Gena slightly exceeding width of compound eye; ocelloccipital distance equalling diameter of lateral ocellus. Fovea dorsally narrow, occupying ¼ space between lateral ocellus and compound eye, ventrally extending below level of antennal insertions, consistently wide along its length, filled with white hairs. Face, gena, vertex, and scape covered with sparse whitish hairs, none equalling length of scape. Antennae dark, A3 equalling length of A4+5. ***Mesosoma*:** Scutum and scutellum regularly punctate, punctures separated by 1 puncture diameter, underlying surface shagreened and weakly shiny (Fig. 49C). Pronotum rounded. Mesepisternum microreticulate, weakly shiny with finely raised reticulation. Dorsolateral parts of propodeum with dense network of reticulation; propodeal triangle laterally delineated with raised carinae, internal surface with dense network of raised rugosity. Mesepisternum, scutum, and scutellum with long whitish hairs, none equalling length of scape. Propodeal corbicula incomplete, dorsal fringe composed of long whitish plumose hairs, internal surface with scattered long simple whitish hairs. Legs dark, pubescence whitish to light brownish. Flocculus complete, composed of short weakly upturned plumose hairs; flocculus, femoral and tibial scopae white, tibial scopae with some brown hairs dorso-basally. Hind tibial claws with inner tooth. Wings hyaline, stigma dark brown, venation brown, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas very narrowly lightened hyaline-brown. Tergal discs densely and clearly punctate, disc of T1 with punctures separated

Figure 49. *Andrena* (*Micrandrena*) *ortizi* sp. nov. female **A** profile **B** face, frontal view **C** scutum, dorsal view **D** terga, dorsal view.

by 1 puncture diameter, T2–3 with punctures separated by 0.5 puncture diameters, underlying surface shagreened and weakly shiny (Fig. 49D). Marginal areas impunctate, with rectangular shagreen; marginal areas long, on T1 occupying ¼ of tergum, on T2 occupying ½ of tergum, on T3 occupying 2/3rds of tergum, on T4 occupying almost all visible tergum. T2–4 with long sparse plumose hairs arising from base of marginal area, covering but not obscuring marginal area; T3–4 apically with dense short apical fringe of white hairs laterally, obscuring underlying surface. Apical fringe of T5 and hairs flanking pygidial plate dark brown with occasional whitish hairs laterally; pygidial plate rounded triangular, with obscurely raised medial ridge, otherwise featureless.

Male. Unknown.

Diagnosis. *Andrena ortizi* can quickly be recognised as a *Micrandrena* due to its small body size, dark integument, and entirely rugose propodeal triangle. Due to the comparatively (for a *Micrandrena*) long face and clypeus (head overall only 1.1 times wider than broad; apical margin of clypeus clearly ventrally exceeding level of a line drawn between the lower margins of the compound eyes), narrow facial fovea (dorsally occupying ¼ of space between the lateral ocellus and the compound eye, consistently wide along its length, and densely punctate scutum (punctures separated by <1 puncture diameter) they are comparable to *A. rugulosa* Stöckhert, 1935 (Switzerland to Lebanon

and the Caucasus), *A. atlantea* Wood, 2021 (High and Middle Atlas Mountains in Morocco), and an undescribed *Micrandrena* species from the Middle Atlas (see above).

Andrena ortizi can be separated from *A. rugulosa* by the scutum which is slightly less densely punctate, punctures separated by 1 puncture diameter (punctures separated by 0.5 puncture diameters in *A. rugulosa*), the underlying surface of the scutum being finely shagreened and shiny (scutum is densely shagreened and dull in *A. rugulosa*), the tergal discs are strongly and clearly punctate (tergal discs obscurely punctate in *A. rugulosa*), and the marginal areas of T2–4 occupy at least ½ the visible length of the tergum, on T3–4 clearly occupying over ½ this length (marginal areas typically occupying ⅓ length of tergum, at most occupying ½ tergum on T4 in *A. rugulosa*). *Andrena ortizi* is more similar to *A. atlantea*, sharing a similarly less densely punctate and weakly shiny scutum, but the same character of wide tergal margins can be used to separate them, with the marginal areas occupying at most ⅓ of the length of the tergum in *A. atlantea*. Finally, *A. ortizi* is most similar to the undescribed *Micrandrena* from the Middle Atlas, and the width of the tergal margins can again be used to separate them, with the tergal margins occupying at most ⅓ of the disc of T2 and ½ of the discs of T3–4. Additionally, *A. ortizi* has the disc of T2–3 clearly and densely punctate, whereas in the undescribed *Micrandrena* the discs of T2–3 are at most obscurely punctate, with punctures disappearing into the background microreticulation. *Andrena ortizi* also has a strongly isolated distribution, separated from the Swiss Alps (*A. rugulosa*) by c. 1,300 km and the high altitude parts around Ifrane and Azrou in the Middle Atlas (*A. atlantea*, the undescribed *Micrandrena* species) by c. 400 km.

Remarks. At the Mirador Monte Ahí de Cara (Fig. 50A, see also Fig. 22A), this species was collected foraging for pollen on the spiny yellow species *Vella spinosa* (Brassicaceae) in open habitat just above the tree line. *Andrena ortizi* appears to be endemic to the Sierra Nevada. Searches at elevations lower than 2000 m did not detect the species during 2021 surveys, so the collection nominally made at 1300 m near Órgiva may not be representative – the slopes above Órgiva (southern slopes of the Sierra Nevada) ascend rapidly, the collector may well have climbed to a higher altitude when collecting this specimen. The morphological similarity between *A. rugulosa*, *A. ortizi*, and *A. atlantea* suggests a pattern of geographical isolation in montane habitats, though only *A. ortizi* and *A. atlantea* show a close genetic relationship based on the COI sequences.

Etymology. Dedicated to the Spanish naturalist and hymenopterist Francisco Javier Ortiz-Sánchez who has worked extensively on the Iberian bee fauna for many years, including that of the Sierra Nevada.

Distribution. Spain (Sierra Nevada).

Andrena (*Truncandrena*) *ghisbaini* Wood, sp. nov.

https://zoobank.org/E5ABB0AB-EE49-4CCC-91B4-9A9A99AD2A5C

Type material. ***Holotype.*** **Spain:** Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 36.6621°N, -5.0362°W, 1600 m, 30.v.2021, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW239-21].

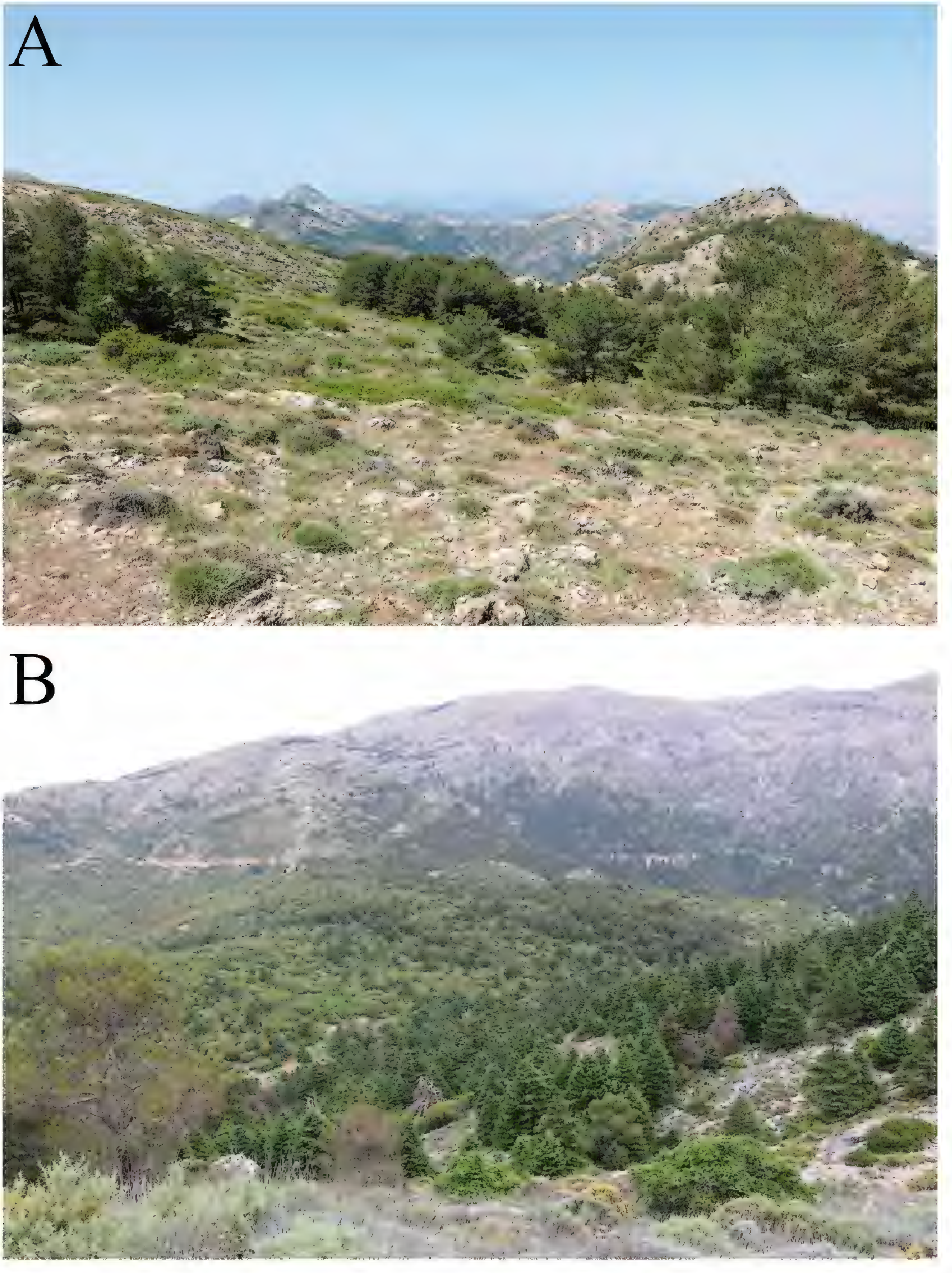

Figure 50. Habitat context **A** *Andrena* (*Micrandrena*) *ortizi* sp. nov., Granada, Sierra Nevada, Mirador Monte Ahí de Cara, 2100 m, 12.vi.2021 **B** *Andrena* (*Truncandrena*) *ghisbaini* sp. nov., Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 1600 m, 30.v.2021.

Paratypes. **Spain:** Málaga, PN Sierra de las Nieves, mountain peak S of Pinsapo Escalereta, 1600 m, 30.v.2021, 1♀, leg. G. Ghisbain, TJWC; Málaga – Elvira, 11.ii.1981, 4♂, leg. H. Teunissen, RMNH.

Figure 51. *Andrena* (*Truncandrena*) *ghisbaini* sp. nov. female **A** profile **B** face, frontal view **C** terga, dorsal view **D** tibial scopa, profile view.

Description. Female. Body length: 15–16 mm (Fig. 51A). ***Head*:** Dark, 1.2 times wider than long (Fig. 51B). Clypeus weakly domed, clearly punctate, punctures separated by 0.5–1 puncture diameters with exception of median longitudinal impunctate line, narrow basally, broadening apically, thus elongate triangular; underlying surface finely shagreened, weakly shiny. Process of labrum broadly trapezoidal, twice as broad as long, apical margin clearly emarginate. Gena broad, almost two times width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Fovea dorsally occupying slightly more than ½ space between lateral ocellus and compound eye, extending ventrally to lower margins of antennal insertions, filled with black hairs. Gena ventrally and laterally with long light brown hairs, longest equalling length of scape, hairs becoming black on vertex, scape, and majority of face, with shorter light brown hairs around antennae insertions. Antennae basally dark, A4 apically, A5–12 ventrally extensively lightened orange; A3 exceeding A4+5, shorter than A4+5+6. ***Mesosoma*:** Scutum and scutellum with extremely shallow and obscure punctures, punctures separated by 0.5–1 puncture diameters, punctures disappearing into underlying fine granular shagreen, surface dull to very weakly shiny. Pronotum rounded. Mesepisternum and dorsolateral parts of propodeum with fine granular shagreen, weakly shiny, with fine and scattered raised hair-bearing punctures, punctures separated by 2–3

puncture diameters; propodeal triangle broad, with extremely fine granular shagreen, without hair-bearing punctures, propodeal triangle thus defined by change in surface sculpture from dorsolateral parts of propodeum. Mesepisternum and propodeum with long finely plumose light brown hairs, clearly exceeding length of scape; scutum and scutellum medially with long black hairs and occasional isolated pale hairs covering majority of disc, laterally becoming intermixed with light brown hairs. Propodeal corbicula incomplete, very weakly defined, dorsal fringe not differentiated from hairs of internal surface, both parts composed of long finely plumose long light brown hairs. Legs dark, apical tarsal segments lightened dark reddish, pubescence dark brown. Flocculus complete, composed of long weakly plumose and upturned light brown hairs; femoral scopae composed of light brown simple hairs; tibial scopa long, hairs exceeding apical width of hind tibia, hairs dorsally dark brown, ventrally golden orange (Fig. 51D). Hind tarsal claws with inner tooth. Wings hyaline, stigma dark brown, venation dark brown to orange, nervulus interstitial. ***Metasoma*:** Terga dark, apical rim of marginal areas narrowly lightened hyaline-yellow; discs with extremely fine granular shagreen, weakly shiny, with fine and scattered hair-bearing punctures, punctures separated by 3–4 puncture diameters (Fig. 51C). Disc of T1 with long light brown hairs, exceeding length of scape, decreasing in length over T2–3, disc of T3 with intermixed short light brown and black hairs, becoming predominantly black on discs of T4–5. T2–4 with weak apical fringes of short light brown hairs, not obscuring underlying surface. Apical fringe of T5 and hairs flanking pygidial plate dark brown, pygidial plate rounded triangular, with weakly raised medial area, otherwise featureless.

Male. Body length: 13–14 mm (Fig. 52A). ***Head*:** Dark, 1.3 times wider than long (Fig. 52B). Clypeus weakly domed, entirely yellow-marked with exception of two dark rounded spots medio-laterally. Clypeus punctured, punctures separated by 0.5–1 puncture diameters with exception of median longitudinal impunctate line, essentially non-existent basally, broadening apically, thus elongate triangular; underlying surface finely shagreened, weakly shiny. Process of labrum broadly rectangular, 2.5 times wider than long, apical margin weakly emarginate, surface smooth and shiny. Gena broad, 2 times width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Gena ventrally and laterally with long light brown hairs clearly exceeding length of scape, becoming intermixed with black hairs on vertex. Face medially with extensive whitish to light-brownish hairs on clypeus, antennae insertions, and scape intermixed with black hairs along inner margins of compound eyes and scape. Antennae basally dark, A4–13 ventrally lightened orange; A3 longer than A4, shorter than A4+5; A4 rectangular, longer than broad, slightly shorter than A5. ***Mesosoma*:** Mesosoma structurally as in female; pubescence as in female. Legs basally dark, apical tarsal segments and hind tibiae lightened dark reddish-brown, pubescence dark brown to orange brown. Hind tarsal claws with inner tooth. Wings hyaline, stigma orange, venation dark brown to orange, nervulus interstitial. ***Metasoma*:** Terga structurally as in female. Discs of T1–4 with long light brown hair, on T1 clearly exceeding length of scape, becoming progressively shorter to T4; T5–6 with short black hairs on disc (Fig. 52C). T2–4 with weak apical hair fringes apically, not

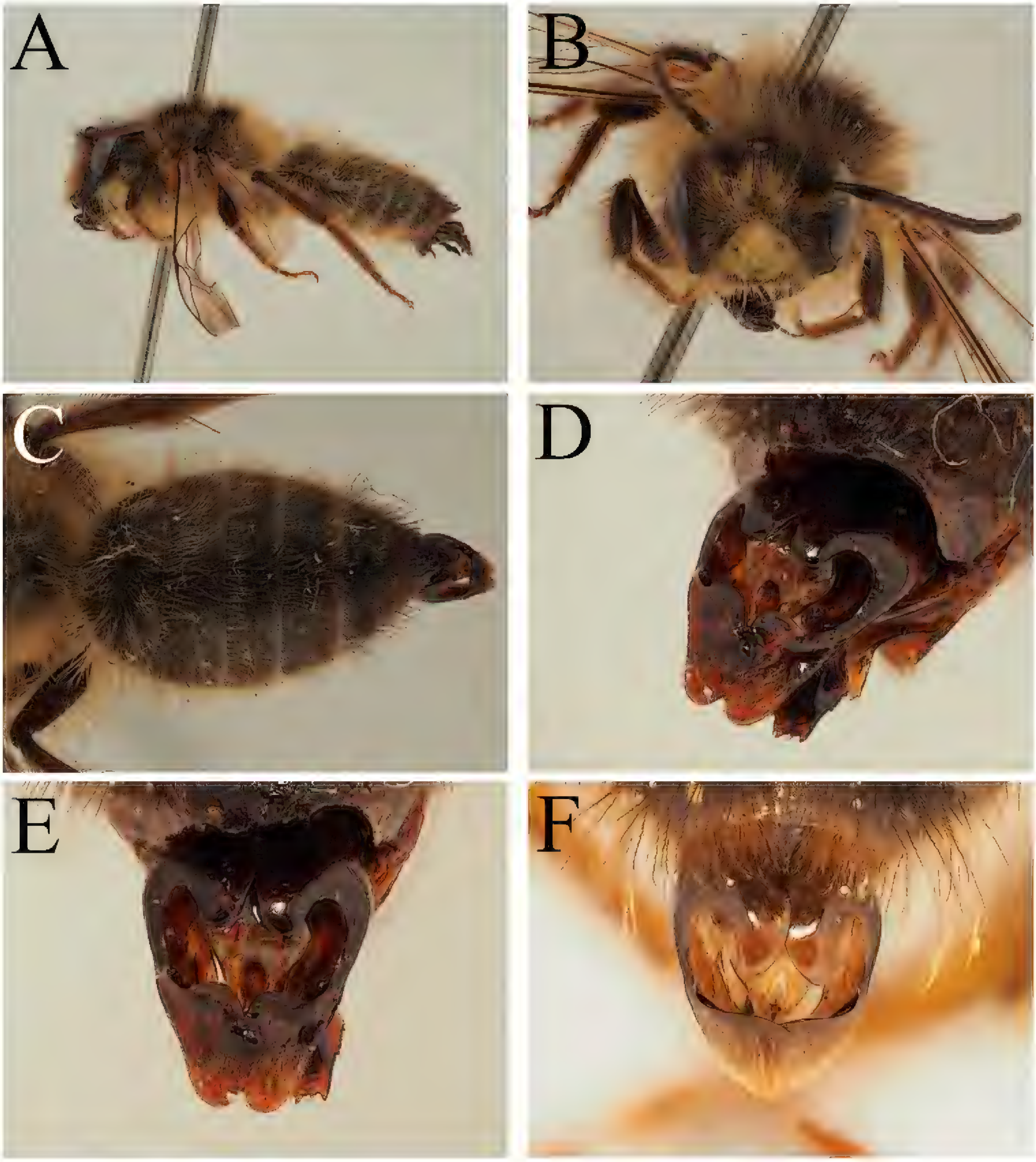

Figure 52. *Andrena* (*Truncandrena*) *ghisbaini* sp. nov. male **A** profile **B** face, frontal view **C** terga, dorsal view **D** genital capsule, dorsolateral view **E** genital capsule, dorsal view; *Andrena* (*Truncandrena*) *villipes* Pérez, 1895 male **F** genital capsule, dorsal view.

obscuring underlying surface. S8 columnar, apex rounded, ventral surface covered with short brown hairs. Genital capsule slightly elongate, gonocoxae produced into strong apical teeth, teeth pointed with apical margins diverging (Fig. 52D, E). Gonostyli basally narrow, apically produced and flattened into rounded triangular plates, internal margin strongly raised and reflexed. Penis valves basally broad, occupying more than ½ space between gonostyli, with narrow laterally produced hyaline extensions; penis valves strongly narrowing apically.

Diagnosis. *Andrena ghisbaini* can be recognised within *Truncandrena* due to its characteristically smooth and finely granulate propodeal triangle which contrasts with the similarly granulate dorsolateral parts of the propodeum which bear fine and scattered raised hair-bearing punctures, the rounded pronotum, the linear malar space, the large body size (>13 mm), yellow male clypeus, and typical genital capsule with the inner margins of the flattened apical parts of the gonostyli strongly raised. It can be placed closest to *A. villipes* Pérez, 1895 (Fig. 30) due to the antennae that are ventrally extensively lightened orange, the intermixed light and dark pubescence of the face, with pale hairs medially and dark hairs laterally, the intermixed light and dark pubescence of the scutum, with dark hairs medially and lighter hairs laterally, by the entirely yellow-marked male clypeus, and by the penis valves basally broad with lateral hyaline extensions, valves strongly narrowing apically.

The immediate difference between the two taxa is size, with *A. villipes* averaging 12–13 mm in length in females and 11–12 mm in males, compared to 15–16 mm and 13–14 mm respectively in *A. ghisbaini*. Structurally, *A. ghisbaini* females can be separated by the bicoloured scopa, black dorsally and orange ventrally (Fig. 51D; *A. villipes* with scopa unicolourous orange, Fig. 30B), the longer face, clypeus clearly projecting ventrally well below a line drawn between the lower margins of the compound eyes (*A. villipes* with face shorter, clypeus only slightly projecting below this line in direct comparison), the clypeus clearly punctured with a longitudinal impunctate midline that broadens apically (*A. villipes* with clypeus obscurely and shallowly punctate, without obvious impunctate midline), and the reduced pale pubescence of the face, with light hairs restricted to the area around the antennal insertions (*A. villipes* with extensive pale hairs covering majority of face and clypeus, with black hairs predominantly along the inner margins of the compound eyes).

In the male sex, *A. ghisbaini* can be separated by the same clypeal punctation character (stronger in *A. ghisbaini* with clearer impunctate midline), but this is slightly more subtle than in the female sex. Direct comparison of the genital capsule shows that flattened apical part of the gonostyli are more strongly elongate and longer than broad, thus appearing triangular (Fig. 52D, E; in *A. villipes* with the flattened apical part of the gonostyli more rounded, about as long as broad, Fig. 52F), the inner margins of these parts more strongly and acutely raised, slightly reflexed (in *A. villipes* with the inner margin less strongly raised and not reflexed).

Remarks. The two females from the Sierra de las Nieves (Fig. 50B) were collected from *Cistus albidus* Linnaeus (Cistaceae). Like *A. villipes* (Table 1), this species is likely to be oligolectic on Cistaceae. Additional surveys are needed to clarify the limits of its range. Male specimens from Elvira in the Naturalis collection were incorrectly determined by Teunissen as *A. maroccana* Benoist, 1950 which is a synonym of *A. leptopyga* Pérez, 1895.

Etymology. Dedicated to my friend and colleague Guillaume Ghisbain (Mons, Belgium) who accompanied me during fieldwork in Málaga province, and who is an accomplished hymenopterist in his own right.

Distribution. Spain (Málaga province).

Table 1. Host plant use and dietary classification for selected Iberian *Andrena* species. *n*, total number of pollen loads; *N*, number of pollen loads from different localities. Plant taxa: ADO, Adoxaceae; AMA, Amaryllidaceae; API, Apiaceae; ASP, Asparagaceae; AST, Asteraceae; BOR, Boraginaceae; BRA, Brassicaceae; CAM, Campanulaceae; CAP, Caprifoliaceae; CAR, Caryophyllaceae; CIS, Cistaceae; CRA, Crassulaceae; EUP, Euphorbiaceae; FAB, Fabaceae; FAG, Fagaceae; FRA, Frankeniaceae; GER, Geraniaceae; HYP, Hypericaceae; PAP, Papaveraceae; PLA, Plantaginaceae; PLU, Plumbaginaceae; RES, Resedaceae; RHA, Rhamnaceae; ROS, Rosaceae; SAL, Salicaceae; SAP, Sapindaceae; SCR, Scrophulariaceae. Countries: BE, Belgium; BG, Bulgaria; DZ, Algeria; ESP, Spain; FRA, France; IL, Israel; IR, Iran; MA, Morocco; PT, Portugal; SY, Syria; TJ, Tajikistan; TN, Tunisia.

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Aciandrena Warncke							
A. fulica Warncke	12	7	ESP (10), PT (2)	BRA 99.6, CIS 0.4	91.7	100.0	Broadly oligolectic (Brassicaceae)
A. vacella Warncke	2	2	ESP (2)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
aegyptiaca-group							
A. alluaudi Benoist	4	3	MA (2), PT (2)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
Aenandrena Warncke							
A. aeneiventris Morawitz	15	7	ESP (15)	API 100.0	100.0	100.0	Possibly broadly oligolectic (Apiaceae)
A. hedikae Jäger	22	10	ESP (11), MA (9), PT (2)	API 100.0	100.0	100.0	Possibly broadly oligolectic (Apiaceae)
A. hystrix Schmiedeknecht	9	5	ESP (8), PT (1)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
Avandrena Warncke							
A. avara Warncke	2	2	ESP (2)	GER 100.0	100.0	100.0	Broadly oligolectic (Geraniaceae)
A. melacana Warncke	6	2	ESP (6)	GER 100.0	100.0	100.0	Broadly oligolectic (Geraniaceae)
A. panurgina De Steffani	11	5	ESP (4), FRA (4), PT (3)	GER 93.6, AST 5.0, BRA 1.4	81.8	100.0	Broadly oligolectic (Geraniaceae)
Blandandrena subgen. nov.							
A. blanda Pérez	27	9	ESP (8), MA (19)	RES 100.0	100.0	100.0	Narrowly oligolectic (*Reseda*, Resedaceae)
Brachyandrena Pittioni							
A. colletiformis Morawitz	6	4	ESP (5), PT (1)	API 100.0	100.0	100.0	Possibly broadly oligolectic (Apiaceae)
A. miegiella Dours	5	4	ESP (2), MA (2), TN (1)	API 99.8, AST 0.2	80.0	100.0	Possibly broadly oligolectic (Apiaceae)
Chlorandrena Pérez							
A. abrupta Warncke	1	1	PT (1)	AST 100.0	100.0	100.0	Probably broadly oligolectic (Asteraceae; Asteroideae)
A. cinerea Brullé	22	15	ESP (6), FRA (3), PT (12), TN (1)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
A. curtivalvis Morice	1	1	ESP (1)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
A. elata Warncke	13	5	ESP (13)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Asteroideae)
A. leucolippa Pérez	22	10	ESP (12), FRA (10)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Asteroideae)
A. rhenana Stöckhert	8	4	ESP (2), PT (6)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
A. senecionis Pérez	21	15	ESP (11), FRA (3), MA (3), PT (4)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)
Chrysandrena Hedicke							
A. fertoni Pérez	4	3	ESP (4)	AST 100.0	100.0	100.0	Broadly oligolectic (Asteraceae; Cichorioideae)

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
Cordandrena Warncke							
A. vaulogeri Pérez	10	5	ESP (3), MA (7)	BRA 61.8, ROS 22.6, AST 9.6, FAB 6.0	30.0	80.0	Polylectic s. str.
Cryptandrena Pittioni							
A. ventricosa Dours	39	10	ESP (29), FRA (10)	FAB 92.8, API 6.1, others 1.1	76.9	97.4	Polylectic with a strong preference (Fabaceae)
Didonia Gribodo							
A. mucida Kriechbaumer (1st generation)	3	3	ESP (1), PT (2)	ASP 100.0	100.0	100.0	Possibly narrowly oligolectic (*Muscari*; Asparagaceae)
A. mucida Kriechbaumer (2nd generation)	12	8	BG (2), ESP (9), MA (1)	CAP 100.0	100.0	100.0	Broadly oligolectic (Caprifoliaceae)
Euandrena Pérez							
A. lavandulae Pérez	5	5	ESP (3), FRA (1), PT (1)	FAB 27.6, CIS 24.3, SCR 20.7, PLA 10.3, AST 8.3, CAM 4.7, GER 2.9, CAR 1.2	20.0	20.0	Polylectic s. str.
Graecandrena Warncke							
A. nebularia Warncke	5	3	ESP (1), MA (4)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
A. verticalis Pérez	30	21	ESP (20), MA (8), PT (2)	BRA 56.3, API 43.8	53.3	53.3	Mesolectic (Apiaceae & Brassicaceae)
incisa-group							
A. lateralis Morawitz	7	3	ESP (3), IR (1), TJ (3)	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)
Leucandrena Hedicke							
A. leptopyga Pérez	19	12	DZ (1), ESP (1), MA (12), PT (5)	RES 90.8, BRA 6.6, BOR 1.8, SCR 0.7	78.9	94.7	Polylectic with a strong preference (*Reseda*, Resedaceae)
A. tunetana Schmiedeknecht	4	4	DZ (1), ESP (2), MA (1)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
Melanapis Cameron							
A. fuscosa Erichson	18	12	ESP (15), FRA (1), IL (1), PT (1)	BRA 52.4, API 15.5, PAP 12.7, AST 9.5, ROS 6.1, EUP 3.1, others 0.7	50.0	72.2	Polylectic s. str.
Melandrena Pérez							
A. albopunctata (Rossi)	15	7	ESP (14), MA (1)	AST 47.4, API 25.3, CAP 11.2, BRA 6.4, FAB 3.9, PAP 3.1, others 2.7	20.0	86.7	Polylectic s. str.
A. assimilis Radoszkowski	15	6	ESP (4), FRA (11)	AST 34.8, ROS 21.1, API 21.0, PLU 7.9, AMA 6.6, SAL 2.7, others 6.1	6.7	73.3	Polylectic s. str.
A. bicolorata (Rossi)	8	5	ESP (2), PT (6)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. florentina Magretti	9	5	MA (1), PT (8)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. morio Brullé (including *A. hispania* Warncke)	9	8	ESP (3), PT (6)	CIS 69.6, API 17.2, AST 10.0, others 3.2	22.2	77.8	Polylectic s. str.
Micrandrena Ashmead							
A. ampla Warncke	21	10	ESP (10), FRA (10), PT (1)	API 100.0	100.0	100.0	Broadly oligolectic (Apiaceae)
A. bayona Warncke	2	2	ESP (2)	API 50.0, BRA 50.0	50.0	50.0	Probably polylectic
A. djelfensis Pérez	20	13	ESP (3), MA (7), PT (10)	CIS 99.9, FAB 0.1	95.0	100.0	Broadly oligolectic (Cistaceae)
A. fabrella Pérez	22	13	ESP (8), FRA (1), MA (5), PT (8)	CIST 99.9, AST 0.1	90.0	100.0	Broadly oligolectic (Cistaceae)

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
A. icterina Warncke	9	6	ESP (9)	BRA 69.1, CIS 10.6, SAL 10.3, EUP 5.8, others 4.2	22.2	88.9	Polylectic s. str.
A. longibarbis Pérez	13	8	ESP (2), MA (8), PT (3)	BRA 99.6, AST 0.4	92.3	100.0	Broadly oligolectic (Brassicaceae)
A. nana (Kirby)	51	28	ESP (33), FRA (1), MA (8), PT (9)	API 71.2, BRA 28.6, EUP 0.2	68.6	74.5	Polylectic with a strong preference (Apiaceae)
A. nitidula Pérez	39	18	ESP (16), MA (21), PT (2)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. omnilaevis Wood	6	5	ESP (2), PT (4)	CRA 100.0	100.0	100.0	Probably narrowly oligolectic (*Sedum*, Crassulaceae)
A. orana Warncke	17	3	DZ (9), MA (5), PT (3)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. pauxilla Stöckhert	11	5	ESP (11)	CRA 82.1, BRA 17.9	81.8	81.8	Possibly polylectic with a strong preference (*Sedum*, Crassulaceae)
A. spreta Pérez	19	11	ESP (15), MA (3), PT (1)	BRA 93.1, AST 3.0, EUP 2.8, FAB 1.2	78.9	100.0	Polylectic with a strong preference (Brassicaceae)
A. tenuistriata Pérez	39	27	ESP (17), FRA (3), MA (6), PT (13)	BRA 99.8, others 0.2	94.9	100.0	Broadly oligolectic (Brassicaceae)
Nobandrena Warncke							
A. funerea Warncke	12	6	ESP (12)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
Notandrena Pérez							
A. aerinifrons Dours	25	8	DZ (3), ESP (3), MA (11), PT (8)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. bellidis Pérez	3	3	ESP (2), PT (1)	AST 38.9, RES 36.4, RAN 18.2, BOR 6.5	0.0	66.7	Polylectic s. str.
A. juliana Wood	35	2	ESP (35)	API 82.6, FRA 13.1, CIS 2.8, others 1.4	74.3	82.9	Polylectic with a strong preference (Apiaceae)
A. leucophaea Lepeletier	2	2	ESP (2)	AST 100.0	100.0	100.0	Possibly oligolectic (Asteraceae; Asteroideae)
A. nigroviridula Dours	9	8	ESP (4), MA (4), PT (1)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. varuga Warncke	3	2	ESP (3)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
numida-group							
A. hypopolia Schmiedeknecht	8	7	ESP (4), FRA (1), PT (3)	BRA 64.8, API 34.6, AST 0.6	50.0	62.5	Mesolectic (Apiaceae & Brassicaceae)
A. ranunculorum Morawitz	17	17	FRA (17)	BRA 75.8, API 10.2, ROS 5.7, FAG 5.6, AST 2.1, ADO 0.5	64.7	100.0	Polylectic with a strong preference (Brassicaceae)
Orandrena Warncke							
A. monilia Warncke	2	2	ESP (1), MA (1)	BRA 100.0	100.0	100.0	Probably broadly oligolectic (Brassicaceae)
Ovandrena subgen. nov.							
A. farinosa Pérez	9	5	ESP (9)	FAB 100.0	100.0	100.0	Broadly oligolectic (Fabaceae)
A. oviventris Pérez	28	11	ESP (9), FRA (4), MA (12), PT (3)	RES 98.3, others 1.7	82.1	100.0	Narrowly oligolectic (*Reseda*, Resedaceae)
Plastandrena Hedicke							
A. asperrima Pérez	56	29	ESP (8), FRA (5), MA (43)	BRA 77.6, RES 18.6, ROS 2.5, AST 1.3	69.6	87.5	Polylectic with a strong preference (Brassicaceae)
A. pilipes Fabricius s. str.	28	21	ESP (15), FRA (8), PT (5)	BRA 54.4, ROS 18.9, AST 13.8, CIS 6.6, API 5.7, others 0.7	35.7	57.1	Polylectic s. str.
relata-group							
A. corax Warncke	10	4	ESP (8), PT (2)	RES 99.7, AST 0.3	90.0	100.0	Narrowly oligolectic (*Reseda*, Resedaceae)
A. laurivora Warncke	3	1	MA (1)	RES 100.0	100.0	100.0	Probably narrowly oligolectic (*Reseda*, Resedaceae)

Species	*n*	*N*	Origin (and number) of pollen loads	Result of microscopic analysis of pollen grains (% of pollen grains)	Percentage of pure loads of preferred host	Percentage of loads with preferred host	Host range
A. relata Warncke	2	2	ESP (2)	RES 100.0	100.0	100.0	Probably narrowly oligolectic (*Reseda*, Resedaceae)
Rufandrena Warncke							
A. orbitalis Morawitz	9	6	ESP (2), FRA (4), PT (3)	PLA 100.0	100.0	100.0	Narrowly oligolectic (*Plantago*, Plantaginaceae)
A. rufiventris Lepeletier	3	1	MA (3)	PLA 100.0	100.0	100.0	Narrowly oligolectic (*Plantago*, Plantaginaceae)
Simandrena Pérez							
A. antigana Pérez	25	14	ESP (6), MA (7), PT (12)	BRA 99.8, others 0.2	96.0	100.0	Broadly oligolectic (Brassicaceae)
A. cilissaeformis Pérez	5	5	ESP (2), MA (3)	BRA 83.6, EUP 8.8, RHA 7.6	60.0	80.0	Probably polylectic with a strong preference (Brassicaceae)
A. propinqua Schenck	43	31	BE (4), ESP (21), FRA (5), MA (3), PT (10)	BRA 46.1, ROS 25.8, FAB 10.2, CIS 4.4, CRA 3.2, BOR 2.5, others 7.7	30.2	58.1	Polylectic s. str.
A. rhypara Pérez	4	3	MA (4)	RES 100.0	100.0	100.0	Possibly narrowly oligolectic (*Reseda*; Resedaceae)
A. vetula Lepeletier	31	16	ESP (20), FRA (2), MA (7), SY (1), TN (1)	BRA 99.8, others 0.2	93.5	100.0	Broadly oligolectic (Brassicaceae)
Truncandrena Warncke							
A. doursana Dufour	8	3	MA (7), PT (1)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. ferrugineicrus Dours	28	18	DZ (1), ESP (16), MA (2), PT (9)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. nigropilosa Warncke	23	8	ESP (16), FRA (5), MA (2)	BRA 100.0	100.0	100.0	Broadly oligolectic (Brassicaceae)
A. villipes Pérez	6	2	FRA (1), PT (5)	CIS 100.0	100.0	100.0	Probably broadly oligolectic (Cistaceae)

Description of missing sexes

Andrena (*Micrandrena*) *alma* Warncke, 1975

Description. Male. Body length 6.5–7 mm (Fig. 53A). ***Head*:** Dark, 1.2 times wider than long. Clypeus flattened, unevenly punctate with large punctures, punctures separated by 0.5–2 puncture diameters, underlying surface shagreened in basal half, polished and shiny in apical half. Process of labrum trapezoidal, slightly wider than long, apical margin slightly thickened. Gena 1.3 times width of compound eye (Fig. 53B, C); ocelloccipital distance 0.5 times diameter of lateral ocellus. Face medially with whitish hairs, scape with mixture of black and white hairs, inner margin of compound eyes with black hairs, gena ventrally with white hairs, becoming black dorsolaterally, vertex and frons with mixture of black and pale hairs, none exceeding length of scape. Antennae dark, A3 exceeding length of A4, shorter than A4+5. ***Mesosoma*:** Scutum and scutellum finely granularly shagreened and weakly shiny, shallowly and obscurely punctate, punctures separated by 2–3 puncture diameters. Pronotum with clear humeral angle. Mesepisternum and dorsolateral surfaces of propodeum with fine granular microreticulation, with regular slightly raised hair bearing punctures. Propodeal triangle with regular granular shagreen, basally and medially with obscure and finely raised rugosity, propodeal triangle thus defined by change in surface sculpture compared to dorsolat-

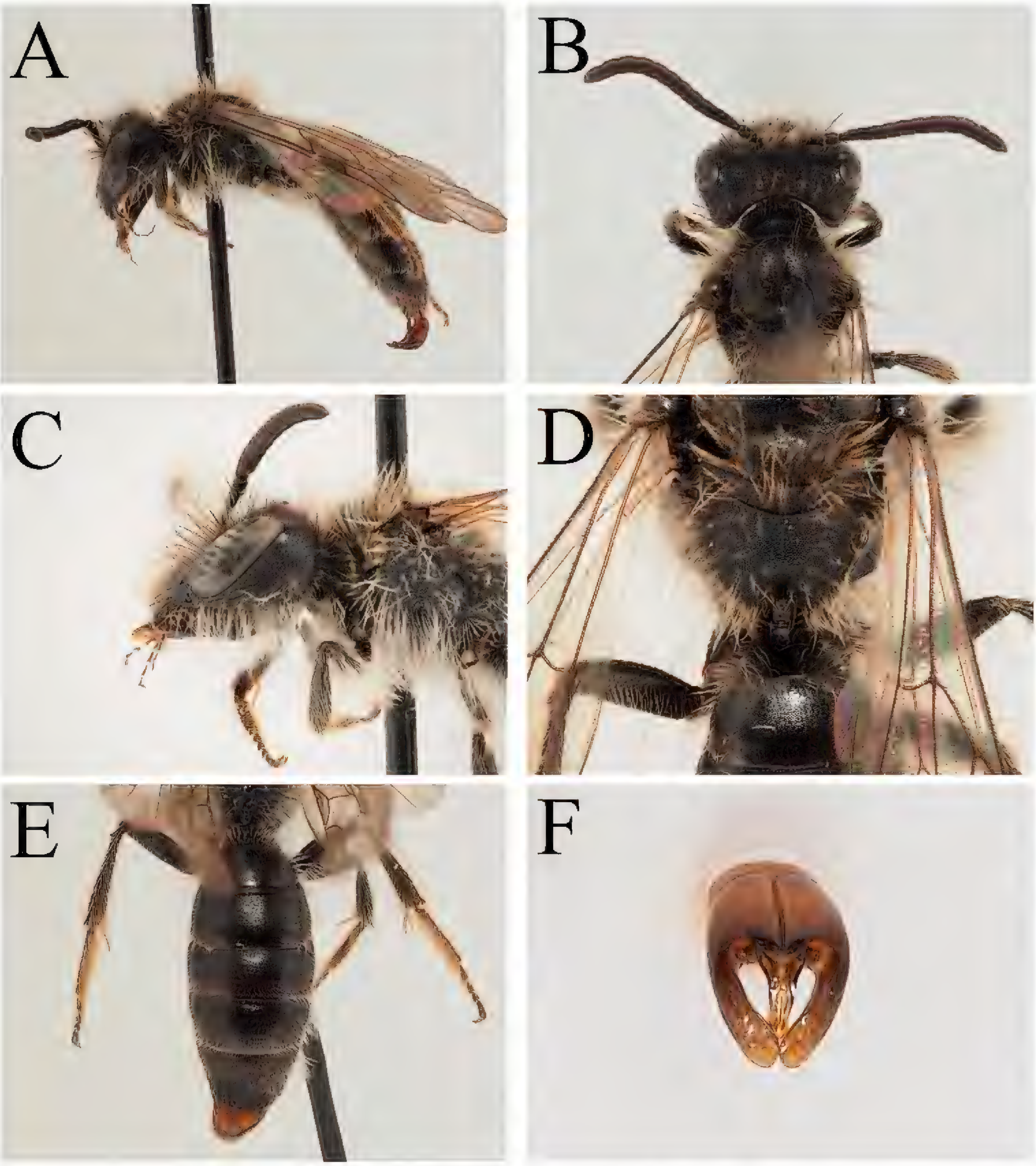

Figure 53. *Andrena* (*Micrandrena*) *alma* Warncke, 1975 male **A** profile **B** head, dorsal view **C** head, profile view **D** propodeal triangle, dorsal view **E** terga, dorsal view **F** genital capsule, dorsal view.

eral parts of propodeum (Fig. 53D). Mesosoma laterally with long white pubescence, exceeding length of scape, pubescence becoming brownish and shorter dorsally, not exceeding length of scape. Legs dark, pubescence whitish. Hind tarsal claws with inner tooth. Wings hyaline, venation and stigma dark brown, nervulus interstitial. ***Metasoma*:** Terga dark, marginal areas obscurely lightened dark hyaline brown apically (Fig. 53E). Tergal discs with obscure and weak punctures that disappear into even underlying microreticulation, surface weakly shiny. Tergal discs with sparse long light brown hairs, T2–4 laterally with weak, widely interrupted apical hair fringes. S8 columnar, slightly

broadened apically, ventrally covered with short yellowish hairs. Genital capsule compact, gonocoxae apically weakly produced into short rounded teeth; gonostyli parallel-sided, spatulate; penis valves slightly broadened basally (Fig. 53F).

Diagnosis. *Andrena alma* can be recognised due to its combination of small body size, dark integument, pronotum with humeral angle, evenly shagreened and weakly shiny terga, gena exceeding the width of the compound eye (Figs 53B, C), flattened and striation-free clypeus, simple genital capsule (Fig. 53F), and smooth and granulate propodeal triangle with obscure and finely raised rugosity basally (Fig. 53D). This smooth propodeal triangle places it close to former *Distandrena* species, but the flattened and striation-free clypeus excludes *A. longibarbis* Pérez, 1895 (clypeus domed, obscurely striate) and *A. orana* Warncke, 1974 (clypeus domed and striate). The evenly shagreened terga and obscure basal rugosity on the largely granularly shagreened propodeal triangle place it superficially close to *A. djelfensis*, but this species can easily be separated by the distinctive genital capsule with elongate and strongly medially bent gonostyli, whereas the genital capsule is simple and lacking distinctive features in *A. alma*. Finally, *A. alma* has a distinctly broadened gena that slightly but distinctly wider than the width of the compound eye, an unusual character in *Micrandrena*. This allows separation from *A. abjecta* which has the gena equalling the width of the compound eye. Collectively, these characters make recognition of *A. alma* straightforward, though as the males of *A. tenostra* and *A.* aff *mica* are unknown, diagnosis may become more challenging in the future. A level of caution should therefore be applied when identifying material from the extreme south and south-east of Spain.

Distribution. Central and southern Portugal and Spain.

Material examined. **Portugal:** Algarve, Monte Gordo, Retur, Praia do Cabeço, 29.iii.2022, 1♂, leg. T.J. Wood, TJWC; Algarve, Tavira, Cacela Velha, 28.iii.2022, 1♂, leg. T.J. Wood, TJWC; **Spain:** Almodóvar del Campo (Ciudad Real), 700 m, 24.iii.2005, 1♂, leg. F.J. Ortiz-Sánchez, FJOS; Santa Ana la Real, Sierra Aracena (Huelva), 630 m, 13.iv.2006, 2♂, leg. F.J. Ortiz-Sánchez, FJOS; El Hongo (P.N. Doñana), 30.iii.2018, 1♂, leg. F. Molina, EBDC.

Andrena (*?Euandrena*) *ramosa* Wood, 2022

Description. Male. Body length 8–10 mm (Fig. 54A). ***Head*:** Dark, 1.05 times wider than long (Fig. 54C). Clypeus long, weakly domed, unevenly punctate, punctures separated by 0.5–2 puncture diameters, underlying surface strongly shagreened to microreticulate in basal half, becoming smooth and shiny in apical half. Process of labrum trapezoidal, 3 times wider than long, ventral surface smooth and polished. Gena equalling width of compound eye; ocelloccipital distance 1.5 times diameter of lateral ocellus. Face medially and gena ventrally with long yellowish hairs, face laterally, frons, and scape with long black hairs, mixing medially on face with yellowish hairs, longest exceeding length of scape. Antennae dark, A3 exceeding length of A4, shorter than A4+5, A4 slightly longer than wide, A5–13 elongate, clearly longer than wide. ***Mesosoma*:** Scutum and scutellum obscurely punctate, punctures separated by 1–2 puncture di-

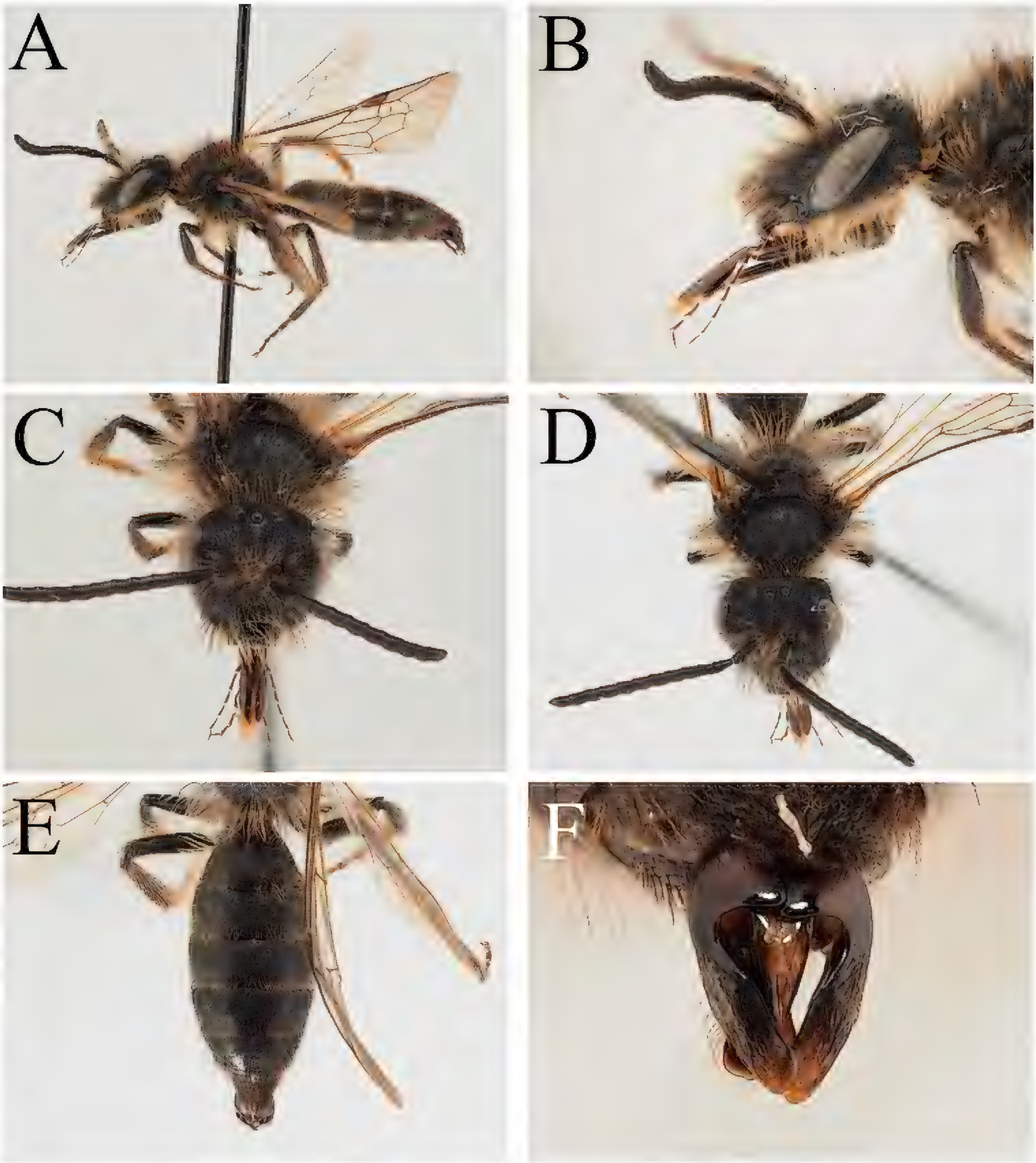

Figure 54. *Andrena* (?*Euandrena*) *ramosa* Wood, 2022 male **A** profile **B** head, profile view **C** head, frontal view **D** scutum, dorsal view **E** terga, dorsal view **F** genital capsule.

ameters, disappearing into extremely strong underlying granular microreticulation, surface dull (Fig. 54D). Pronotum rounded. Mesepisternum and dorsolateral surface of propodeum with fine granular microreticulation, with finely raised network of reticulation that gives impression of large shallow punctures. Propodeal triangle narrow, surface with fine granular shagreen, basally and medially with finely raised rugosity, propodeal triangle thus defined by change in surface sculpture compared to dorsolateral parts of propodeum. Mesosoma with long, densely branches and plumose yellowish hairs clearly exceeding length of scape, black plumose hairs intermixed around wing

bases, on scutum, and propodeum. Legs dark, pubescence brownish to black. Hind tarsal claws with inner tooth. Wings hyaline, stigma dark brown, venation dark to light brown, nervulus weakly antefurcal. ***Metasoma*:** Terga dark, apical rim of marginal areas very narrowly lightened hyaline brown (Fig. 54E). Tergal discs with obscure hair-bearing punctures, disappearing into background sculpture, becoming more strongly defined laterally, underlying surface shagreened and weakly shiny. T1–3 with long but loose plumose yellowish-brown hairs, these becoming black on T4–5. S8 relatively short, rectangular, apically truncate, ventrally covered with dark brown hairs. Genital capsule moderately elongate, gonocoxae apically weakly produced into short rounded projections, gonostyli more or less parallel-sided, spatulate (Fig. 54F). Penis valves occupying ½ space between gonostyli, slightly narrowing towards their apexes.

Diagnosis. The male of *A. ramosa* is morphologically most similar to *A.* (*Euandrena*) *solenopalpa* due to the long head (only marginally wider than long) and clypeus that is shiny at least in its apical half. The two species are easily separated by the mouthparts, as in *A. ramosa* the mouthparts that protrude in front of the head are at most as long as the head (viewed frontally or laterally, Fig. 54B), whereas in *A. solenopalpa* the mouthparts are extremely long, the labial palpi alone exceed the length of their head, the part of the mouthparts protruding in front of the head therefore collectively greatly exceed the length of the head. The clypeus of *A. solenopalpa* is also more extensively shiny, the gonostyli have their outer margin emarginate and are apically produced into narrow points, and A3 slightly exceeds the length of A4+5, whereas in *A. ramosa* the clypeus is shiny only in its apical half, the gonostyli are spatulate and apically truncate, and A3 only slightly exceeds A4, and is shorter than A4+5. The two species do not occur in sympatry, with *A. ramosa* restricted to south-western Spain, whereas *A. solenopalpa* is found in central and eastern Spain to southern France.

Distribution. South-western Spain (Cádiz, Sevilla).

Remarks. The phylogenetic placement of *A. ramosa* remains somewhat obscure even following the discovery of the male sex and generation of a barcode sequence. A 658-bp fragment was generated from the female type specimen [BOLD accession number: IBIHM524-21], but this did not fall unambiguously close to any species or subgenus. The most similar sequences belonged to the subgenus *Euandrena*, specifically to *A. symphyti* (90.26%), *A. montana* Warncke, 1973 (90.31%), *A. fulvida* Schenck, 1853 (89.98%), and *A. rufula* Schmiedeknecht, 1883 (89.84%). Morphologically, *A. ramosa* does not fall nicely into *Euandrena*, as the female sex has foveae which are narrow but which do not narrow ventrally. However, *Euandrena* are part of the most highly derived clade of *Andrena* (Pisanty et al. 2022b), and subgeneric classification in this clade has been highly problematic due to the lack of clear delineating characters. *Andrena ramosa* does not belong to *Margandrena* Warncke, 1968 due to the lack of a strong humeral angle on the pronotum. It does not belong to the *crocusella*-group due to the lack of a humeral angle and the lack of lateral projections on the male penis valves (in addition to the lack of barcode similarity), and whilst it has strongly plumose pollen collecting hairs comprising the propodeal corbiculae and femoral scopae, those of the tibial scopae are simple, and the foveae do not narrow below which makes

placement in *Chrysandrena* Hedicke, 1933 difficult. *Andrena ramosa* is therefore best considered to be affiliated with the subgenus *Euandrena*, pending investigation with more powerful genetic techniques. It clearly possesses a unique and unusual morphology within the West Palaearctic *Andrena* fauna.

Examination of additional material from the province of Cádiz has shown that *A. ramosa* is commonly encountered in the Parque Natural Los Alcornocales area. Here it can be encountered between January and March, and is most frequently observed on *Erica* (Ericaceae; Pérez Gómez in litt.). However, the pollen host is still obscure, since none of these bees have been observed collecting pollen. Moreover, Ericaceae pollen is small, with the grains typically having a diameter of 25 μm. The widely spaced and strongly branched and plumose pollen collecting hairs of *A. ramosa* (described and illustrated by Wood et al. 2022a) would not seem to be an adaptation to the collection of small Ericaceae pollen grains, and indeed this adaptation is absent in the Ericaceae specialist *A.* (*Cnemidandrena*) *fuscipes* (Kirby, 1802) which has simple pollen collecting hairs. Further study is required; the assumption remains that *A. ramosa* collects pollen from a plant species with large pollen grains, thus necessitating these branched and plumose hairs.

Material examined. **Spain:** Carretera Marrufo, Herriza (Cádiz; 3 km E Puerto de Gáliz), 11.xi.2020, 1♀, leg. Á. Pérez Gómez, APGC; Sevilla, Los Pinares de Aznalcázar [37.2782°N, -6.2356°E], 10.iii.2020, 1♀, leg. F. Molina, OÖLM (holotype); Cádiz, Sierra de Montecoche, 31.i.2022, 4♂, 1♀, leg. Á. Pérez Gómez, APGC/TJWC; 18.i.2021, 1♂, leg. Á. Pérez Gómez, APGC; Cádiz, Pico del Montero, 2.ii.2022, 3♂, 1♀, leg. Á. Pérez Gómez, APGC/TJWC; Cádiz, Sierra de Fates, 21.iii.2022, 1♀, leg. Á. Pérez Gómez, APGC; Cádiz, Pico del Montero, Alcalá de los Gazules, 26.iii.2022, 1♂, leg. Á. Pérez Gómez, APGC.

Additional designation of lectotypes

Andrena (*Aenandrena*) *hystrix* Schmiedeknecht, 1883

Andrena (*Aenandrena*) *hystrix* Schmiedeknecht, 1883: 618, ♀ [France, lectotype by present designation: RMNH].

Remarks. Schmiedeknecht (1883) described several *Andrena* species from material that had been sent to him by Pérez. In each case, he indicated this in his title, e.g. 'Andrena hystrix Perez in litt' [sic]. For several of these species, the location of type material has been unclear, as they mostly did not seem to be in the MNHN in the Pérez collection (see Le Divelec 2021), or elsewhere (see Gusenleitner and Schwarz 2002). Searches in the RMNH unexpectedly uncovered specimens of four species described by Schmiedeknecht with labels written in Pérez's distinctive handwriting. The exact providence of these specimens is unclear, but the RMNH collection is known to contain material from Schmiedeknecht's collection (F. Bakker, pers. comm.). A lectotype was designated for one of these species (*A.* (*Andrena*) *mitis* Schmiedeknecht, 1883) in a previous publication (Wood 2023a); the others are designated here.

Schmiedeknecht (1883) described *A. hystrix* from female specimens from Hungary (*Hungaria*) and southern France (*Gallia meridionali*). He did not specify a type, though Gusenleitner and Schwarz (2002) list south France as the *locus typicus*. A specimen of *A. hystrix* from Marseille is labelled with Pérez's handwriting, and this is considered to be part of the original syntypic series; it is here designated as a lectotype (Fig. 55A, B). No specimens from Hungary s.l. could be found.

Material examined. **France:** Marseille [43.3612°N, 5.3942°E], 1♀, RMNH (lectotype by present designation; Fig. 55A, B).

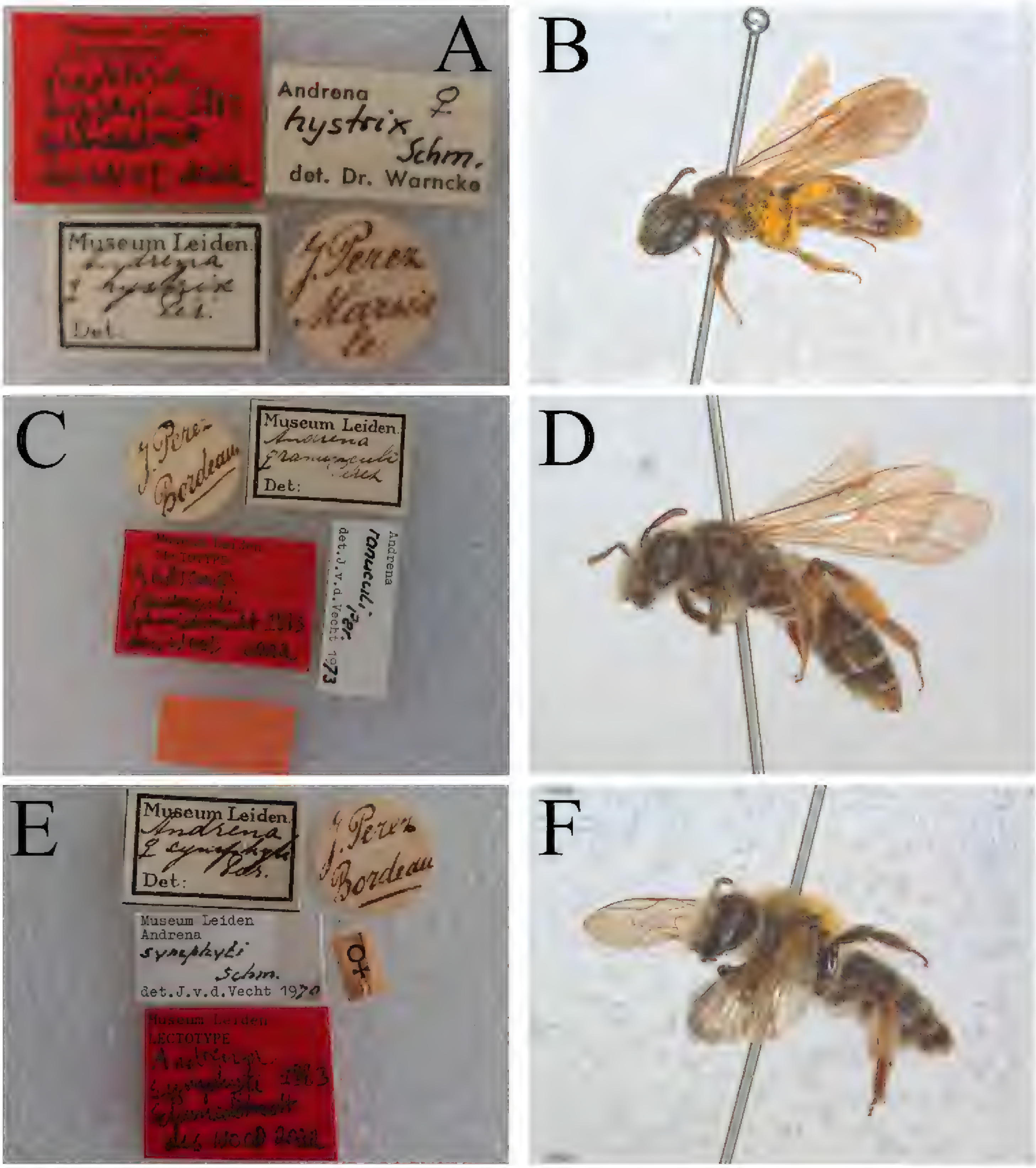

Figure 55. *Andrena* (*Aenandrena*) *hystrix* Schmiedeknecht, 1883, female lectotype **A** label details **B** profile; *Andrena* (*Notandrena*) *ranunculi* Schmiedeknecht, 1883, female lectotype **C** label details **D** profile; *Andrena* (*Euandrena*) *symphyti* Schmiedeknecht, 1883, female lectotype **E** label details **F** profile.

Andrena (*Notandrena*) *ranunculi* Schmiedeknecht, 1883

Andrena (*Notandrena*) *ranunculi* Schmiedeknecht, 1883: 617, ♀♂ [France, lectotype by present designation: RMNH].

Remarks. Schmiedeknecht (1883) described *A. ranunculi*, comparing it to *A. ranunculorum*. He gave the habitat as Russia (referring to *A. ranunculorum*) and southern France (referring to the specimens received from Pérez). A series of males and females labelled by Pérez as being from Bordeau [sic, = Bordeaux] were found in the RMNH. These conform to Schmiedeknecht's description, and the concept used by subsequent authors. A female is here designated as a lectotype (Fig. 55C, D).

Material examined. **France:** Bordeaux [44.8352°N, -0.5888°E], 1♀, RMNH (lectotype by present designation; Fig. 55C, D); Bordeaux, 8♂, 5♀, RMNH.

Andrena (*Euandrena*) *symphyti* Schmiedeknecht, 1883

Andrena (*Euandrena*) *symphyti* Schmiedeknecht, 1883: 583, ♀♂ [France, lectotype by present designation: RMNH].

Remarks. As for the previous two species, material labelled by Pérez was found in the RMNH collection. Two females and one male labelled as being from Bordeau [sic, = Bordeaux]. Schmiedeknecht (1883) specifically states that the type material comes from Bordeaux, writing "*In Gallia prope Bordeaux a Dom. Illustrissimo Perez detecta*". A female is here designated as a lectotype (Fig. 55E, F).

Material examined. **France:** Bordeaux [44.8352°N, -0.5888°E], 1♀, RMNH (lectotype by present designation; Fig. 55E, F); Bordeaux, 1♂, 1♀, RMNH.

Designation of neotypes

Andrena (*Chlorandrena*) *boyerella* Dours, 1872

Andrena (*Chlorandrena*) *distincta* Lucas, 1849 nec. Smith, 1847 [Algeria: MNHN, not examined].
Andrena (*Chlorandrena*) *boyerella* Dours, 1872: 429, ♀♂ [Morocco: OÖLM].

Neotype. **Morocco:** Fès-Meknès, Azrou, 4 km SWW of Bakrit, Cascades Bakrit, 33.0466°N, -5.2681°E, 1650 m, 17.v.2022, 1♂, leg. T.J. Wood, OÖLM [BOLD accession number WPATW495-22] (Fig. 56).

Remarks. As discussed above, Dours (1872) described *A. boyerella* from southern France and Algeria. No material is available for study, as all of Dours' types were destroyed in a fire. Given that two taxa are present in these regions, in order to fix the name *A. boyerella* on the North African population, a barcoded neotype is designated from Moroccan material (Fig. 56).

Distribution. Morocco, Algeria, Tunisia, Italy (Sicily).

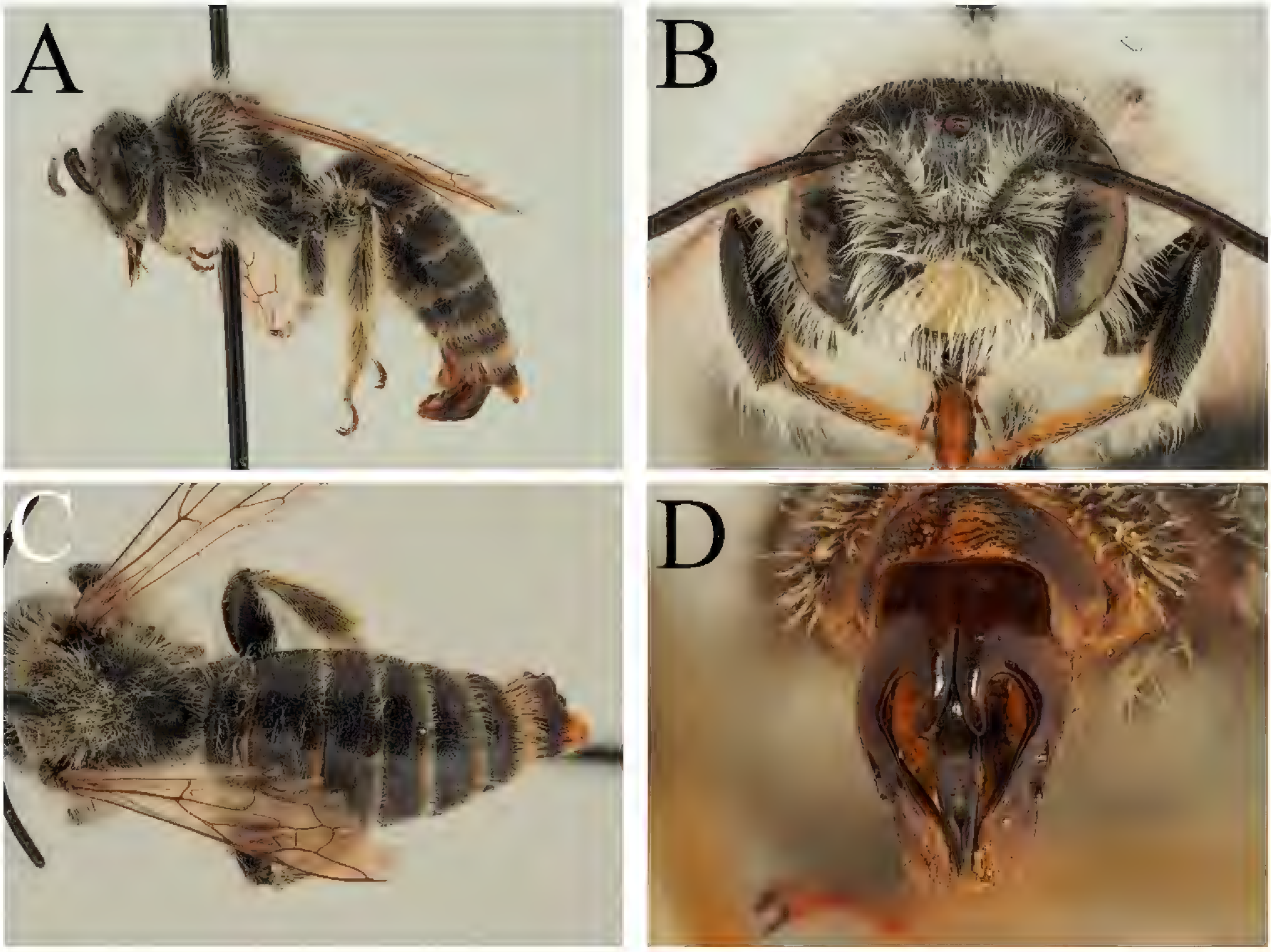

Figure 56. *Andrena* (*Chlorandrena*) *boyerella* Dours, 1872, male neotype **A** profile **B** face, frontal view **C** terga, dorsal view **D** genital capsule dorsal view.

Andrena (*Notandrena*) *griseobalteata* Dours, 1872

Andrena (*Notandrena*) *erythrocnemis* auctorum. nec. Morawitz, 1871.
Andrena (*Notandrena*) *griseobalteata* Dours, 1872: 427, ♀ [France: RMNH].

Neotype. **France:** Pyrénées-Atlantiques, Bérenx [43.4994°N, -0.8575°W], 6.vi.1987, 1♀, leg. E.A.M. Speijer, RMNH (Fig. 57).

Remarks. The correct name to apply to this distinctive taxon has been confused for many years. Through the combination of its large size (for a *Notandrena*) and densely punctate scutum it is comparable only to *A. ungeri* Mavromoustakis, 1952. The name *A. erythrocnemis* Morawitz, 1871 was used by many authors to refer to this taxon (e.g. Warncke 1967), but the lectotype of *A. erythrocnemis* is actually *A. chrysosceles* (see Proshchalykin et al. 2017; Astafurova et al. 2021). Gusenleitner and Schwarz (2002) resolved this issue by resurrecting *A. griseobalteata* to species status. Finally, Wood and Monfared (2022) removed *A. emesiana* Pérez, 1911 (southern Turkey, Syria, Iran) from synonymy with this taxon.

Although Gusenleitner and Schwarz (2002) would seem to have resolved the issue, there is no type specimen for *A. griseobalteata* due to the loss of Dours' collection. In the original description, Dours (1872: 428) listed the species from Saint-Sever in the department of Landes in south-western France, but also from Algeria. This is peculiar,

Figure 57. *Andrena* (*Notandrena*) *griseobalteata* Dours, 1872, female neotype **A** profile **B** face, frontal view **C** scutum, dorsal view **D** terga, dorsal view.

because *A. griseobalteata* is not known from North Africa. The original description also does not allow for completely unambiguous recognition of the species, though the dense punctation of the scutum is mentioned. In the interests of nomenclatural stability, a neotype from Bérenx in south-western France (36 km from Saint-Sever) is designated in order to fix the species concept for the future (Fig. 57).

Finally, though listed from Spain by Ortiz-Sánchez (2011, as *A. griseobalteata*; 2020, as *A. erythrocnemis*), the presence of this taxon in Spain is somewhat doubtful. The distribution maps of Warncke (Gusenleitner and Schwarz 2002) show dots around south-western France into the Pyrenees, but there are no unambiguous dots for Spain. However, I have been able to examine one specimen of *A. griseobalteata* from Spain, from the Sistema Central. The species is also expected to occur in the western Pyrenees; more recent material should be found to establish whether this taxon remains present in Iberia.

Material examined. Spain: Sierra de Gredos, 12 km SSW Hoyos del Espino, 1950–2100 m, 4.vii.1972, 1♀, leg. J.A.W. Lucas, RMNH.

Distribution. Spain, France, Italy, Croatia, Hungary, Albania, Romania, North Macedonia, Bulgaria, Greece, Turkey (western and northern Turkey; Gusenleitner and Schwarz 2002). The species is not considered to be present in North Africa, or in the Levant, as it is not found in very dry environments.

Andrena **(*****Taeniandrena*****)** ***poupillieri*** **Dours, 1872**

Andrena (*Taeniandrena*) *poupillieri* Dours, 1872: 430, ♀ [Algeria: OÖLM].
Andrena (*Taeniandrena*) *poupillieri incana* Warncke, 1975a: 310, ♀♂ [Spain, Mallorca: OÖLM, examined].

Neotype. **Algeria:** Tizi-Ouzou, Tigzirt, 36.8877°N, 4.1140°E, 6 m, 31.iii.2017, 1♀, leg. H. Ikhlef, OÖLM [BOLD accession number HYMAA322-22] (Fig. 58).

Remarks. This is the taxon referred to as '*A. poupillieri* 2' by Praz et al. (2022). The taxon *A. poupillieri incana* Warncke, 1975 which was described from and restricted to the Balearic Islands is considered a simple synonym of *A. poupillieri* due to the lack of genetic differentiation observed (see above), even though the tergal punctation is slightly reduced compared to the nominate taxon. The specimen used in the analysis of Praz et al. (2022) is designated as a lectotype (Fig. 58).

Distribution. Morocco, Algeria, Tunisia, Spain (mainland and Balearic Islands). Records (Gusenleitner and Schwarz 2002) from Libya must be confirmed, though they probably do refer to true *A. poupillieri*. Records from Crete probably refer to unrecognised *A. ovata* specimens, and so *A. poupillieri* is not considered to be present there until definitive material is located.

Figure 58. *Andrena* (*Taeniandrena*) *poupillieri* Dours, 1872, female neotype **A** profile **B** face, frontal view **C** dorsal view **D** terga, dorsal view.

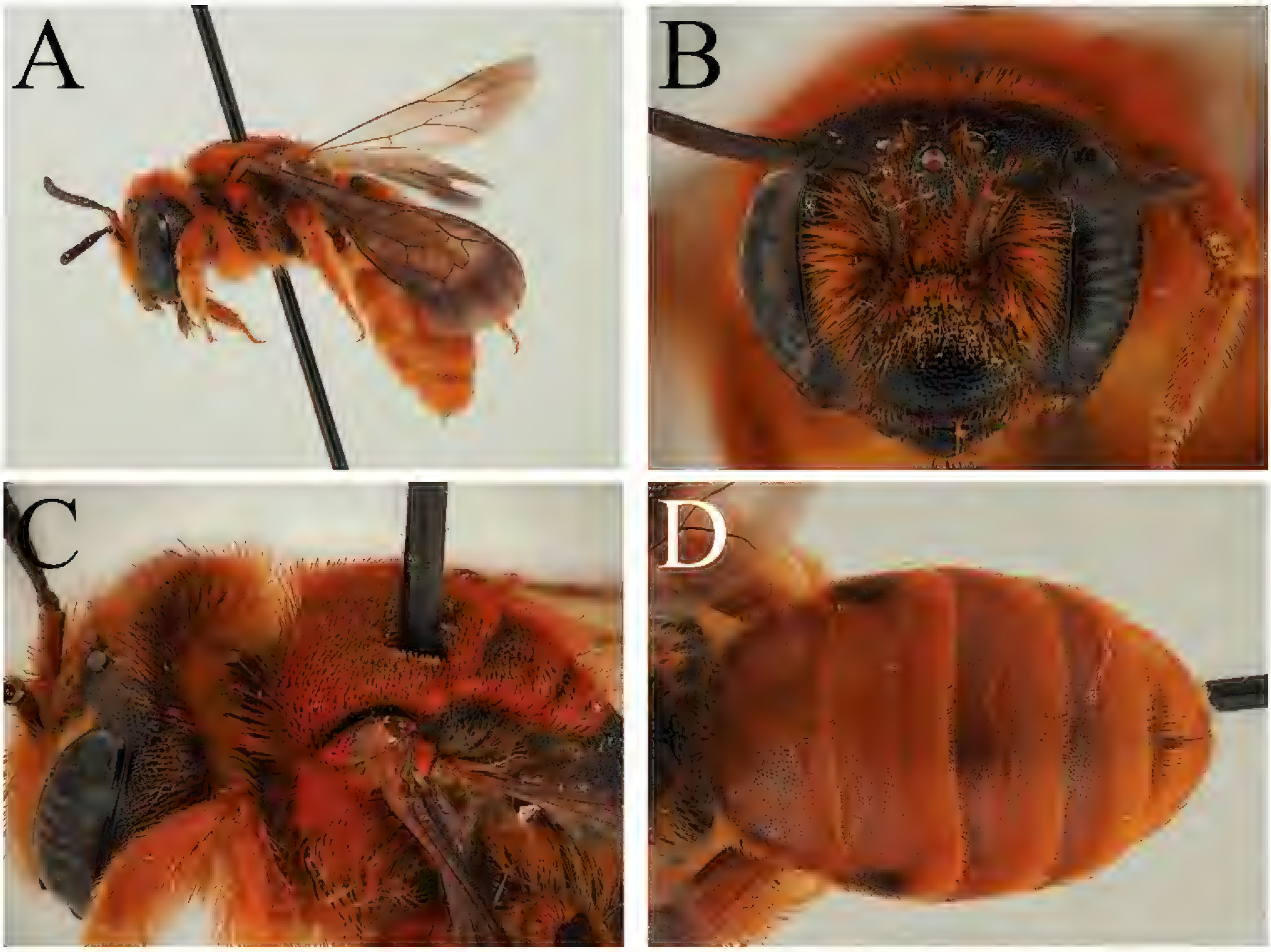

Figure 59. *Andrena* (*Pruinosandrena*) *succinea* Dours, 1872, female neotype **A** profile **B** face, frontal view **C** mesosoma, dorsolateral view **D** terga, dorsal view.

Andrena (*Pruinosandrena*) *succinea* Dours, 1872

Andrena succinea Dours, 1872: 424, ♀ [Morocco: OÖLM].

Neotype. Morocco: Oriental, Guercif, P5427, 2 km SW of Bou Rached, 33.8844°N, -3.6154°W, 950 m, 13.v.2022, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW389-22] (Fig. 59).

Remarks. As discussed above, it is preferable to designate a neotype for *A. succinea* in order to maintain nomenclatural stability. The barcoded specimen pictured in Fig. 34B is selected as a neotype (Fig. 59) in order to fix the species concept for the future.

Distribution. Morocco, Algeria, Tunisia, Libya, Egypt, Israel and the West Bank, Jordan, Syria, Saudi Arabia, Iran (Wood and Monfared 2022).

Andrena (incertae sedis) *numida* Lepeletier, 1841

Andrena numida Lepeletier, 1841: 252, ♀ [Morocco: OÖLM].

Neotype. Morocco: Fès-Meknès, Azrou, P7311, 10 km S of Ain Leuh, 1750 m, 33.2220°N, -5.3411°W, 18.v.2022, 1♀, leg. T.J. Wood, OÖLM [BOLD accession number WPATW484-22] (Fig. 60).

Figure 60. *Andrena* (incertae sedis) *numida* Lepeletier, 1841, female neotype **A** profile **B** face, frontal view **C** dorsal view **D** T2–5, dorsal view detail.

Remarks. As discussed above, it is beneficial to designate a neotype for *A. numida* since the original type series cannot be located in the MNHN, and so that the name and genetic identity of North African populations can be fixed.

Distribution. Morocco, Algeria, Tunisia, Libya, Italy (Sicily, Calabria, Campania).

Updated faunal list

Ortiz-Sánchez (2020) lists 212 species of *Andrena* from Spain. However, given the taxonomic and faunal work that has been conducted since then, this total is slightly too low and contains mistakes resulting from taxonomic confusion and the use of variable species concepts in the literature.

Species removed from baseline list

Following the changes detailed in the previous sections, *A. boyerella*, *A. creberrima*, *A. curtula*, *A. hispania*, *A. mariana* s. str., *A. potentillae*, *A. pusilla*, and *A. truncatilabris* are removed from the Iberian fauna following their listing by Ortiz-Sánchez (2020). Four further species must also be removed, *A. similis* Smith, 1849, *A. enslinella* Stöckhert, 1924, *A. simillima* Smith, 1851, and *A. chrysopyga* Schenck, 1853. *Andrena* (*Taeniandrena*) *similis*

was shown to be a synonym of *A.* (*Taeniandrena*) *russula* Lepeletier, 1841 by Praz et al. (2022). Ortiz-Sánchez (2020) listed both species as present.

Dardón (2010) and Dardón et al. (2014) listed *A.* (*Micrandrena*) aff *enslinella* as present in Spain based on the listing of Warncke (1976) and the specimen in his collection. I do not consider this to be ecologically possible, as *A. enslinella* is a species of Central and Eastern Europe to the Caucasus and Iran, having its western limit in Germany and Austria. The species appears to be absent from France (Le Divelec 2021). Given the highly interesting *Andrena* fauna in the Sistema Ibérico that contains relictual North African taxa such as *A.* (*Cordandrena*) *vaulogeri* Pérez, 1895 and the endemic *A.* (*Parandrenella*) *taxana* Warncke, 1975, further study is required, as this specimen may represent an undescribed species, as suggested by Dardón (2010).

Andrena (*Cnemidandrena*) *simillima* was listed by Ortiz-Sánchez (2020), but not by Warncke (1976). The distribution maps of Warncke (Gusenleitner and Schwarz 2002) give a single isolated dot for this species in north-eastern Spain, presumably in the eastern Pyrenees. The next closest record comes from western France (c. 400 km), with no other records for the Pyrenees. Warncke et al. (1974: carte 140) gave Bordeaux as the south-western limit for *A. simillima* (specimen leg. Pérez, coll. Warncke OÖLM). I consider the dot on the maps of Gusenleitner and Schwarz (2002) to be of doubtful providence; I have examined no material from Iberia of this species, and I could not locate a Spanish specimen in the Warncke collection. No other authors have ever recorded *A. simillima* from the Pyrenees, though *A.* (*Cnemidandrena*) *nigriceps* (Kirby, 1802) is common in this region. Males of *A. simillima* and *A. nigriceps* are extremely difficult to separate, and it is possible that this dot represents a misidentification of *A. nigriceps*. Moreover, this record is ecologically questionable, since *A. simillima* is predominantly a northern species (sensu lato, since cryptic taxa may be present) found in temperate habitats. In the absence of available specimens, the isolated nature of this record, and the identification difficulties associated with this group, I remove *A. simillima* from the Iberian fauna.

Finally, *A.* (*Melandrena*) *chrysopyga* is listed as present in Iberia. I have seen no Iberian material of this taxon which is generally very rare in collections. It is often confused with forms of *A. gravida* with light hairs in the terminal fringe. In the distribution maps of Warncke (Gusenleitner and Schwarz 2002), there are dots for *A. chrysopyga* from south-western France, but none in Iberia proper. *Andrena chrysopyga* is a species of dry grassland and steppe, extending east across the Great Eurasian Steppe to Kazakhstan. Given the absence or scarcity of steppe habitats in France, its presence in much of the country seems ecologically unlikely. Given the overly generous distribution of *A. chrysopyga* given by Warncke (e.g. the species is known only from the extreme east of Belgium yet Warncke's map indicates the presence of this taxon throughout Belgium, see Wood 2023a), the lack of available specimens, and the identification mistakes known to occur between *A. chrysopyga* and *A. gravida*, *A. chrysopyga* is not considered to be part of the Iberian fauna until such a time as validated specimens can be found or the species can be newly captured. Its historical and contemporary distribution in France must also be clarified, as I believe that most records are misidentifications of *A. gravida*.

Species added to baseline list

In addition to the species elevated above or newly described below, the following 15 *Andrena* species were explicitly added to the Iberian fauna by the following works: *A.* (incertae sedis) *laurivora*, *A.* (*Notandrena*) *juliana* Wood, 2021, *A.* (*Euandrena*) *fortipunctata* Wood, 2021, *A.* (*Taeniandrena*) *benoisti* Wood & Praz, 2021, and *A.* (*Taeniandrena*) *levante* Wood & Praz, 2021 (Wood et al. 2021); *A.* (*Plastandrena*) *nigrospina* Thomson, 1872 (Ortiz-Sánchez et al. 2022); *A.* (*Taeniandrena*) *afzeliella* (Kirby, 1802) and *A.* (*Taeniandrena*) *ovata* Schenck, 1853 (Praz et al. 2022); *A.* (*Avandrena*) *erodiorum* Wood & Ortiz-Sánchez, 2022, *A.* (*Avandrena*) *melacana* Warncke, 1967, *A.* (*Taeniandrena*) *lusitania* Wood & Ortiz-Sánchez, 2022, and *A.* (*Suandrena*) *gades* Wood & Ortiz-Sánchez, 2022 (Wood & Ortiz-Sánchez, 2022); *A.* (incertae sedis) *ramosa* Wood, 2022 (Wood et al. 2022a); *A.* (*Taeniandrena*) *contracta* Wood, 2022 (Wood 2022); and *A.* (*Andrena*) *clarkella* (Kirby, 1802) (Álvarez Fidalgo and Aguado Martín 2022).

Therefore, relative to the baseline of Ortiz-Sánchez (2020), 12 species are removed, and 28 species are added (including *Andrena* aff *mica*). In sum, the taxonomic changes and faunal updates presented here and in the referenced papers brings the Iberian *Andrena* fauna to 228 species, a substantial increase on the 175 species recorded by Warncke (1975a), with 228 species known from mainland Spain and 128 species from mainland Portugal. A full checklist can be found in Suppl. material 1.

Dietary niche of Iberian *Andrena* species

Results are presented here for Iberian species for which no or very little previous dietary data have been published. Consequently, these results are not comprehensive, but it is not considered necessary to duplicate here previous analyses that have been conducted in Central Europe (e.g. Westrich 1989) when these same species do not differ in their pollen foraging behaviour in Iberia. Pollen was analysed and removed from a total of 1,127 specimens from 76 species from 12 countries. Findings are summarised in Table 1. *Andrena* species are grouped by subgenus to highlight their often conserved patterns of pollen collection.

Demonstration of oligolecty in understudied species

For many Iberian endemic or West Mediterranean species, an oligolectic dietary niche was clearly and unambiguously demonstrated by pollen analysis. In many cases, specialised pollen use was as expected based on known subgeneric traits, such as the exclusive use of Asteraceae by the subgenus *Chlorandrena* and Brassicaceae by the subgenera *Aciandrena* and *Nobandrena* Warncke, 1968.

It is important to note some pollen collection preferences. Within the *Notandrena*, members of the former *Carandrena* are typically associated with Brassicaceae such as *A. aerinifrons* (Fig. 61A). However, two species deviate from this pattern, *A. bellidis* Pérez, 1895 and *A. leucophaea* Lepeletier, 1841. *Andrena bellidis* appears to be polylectic,

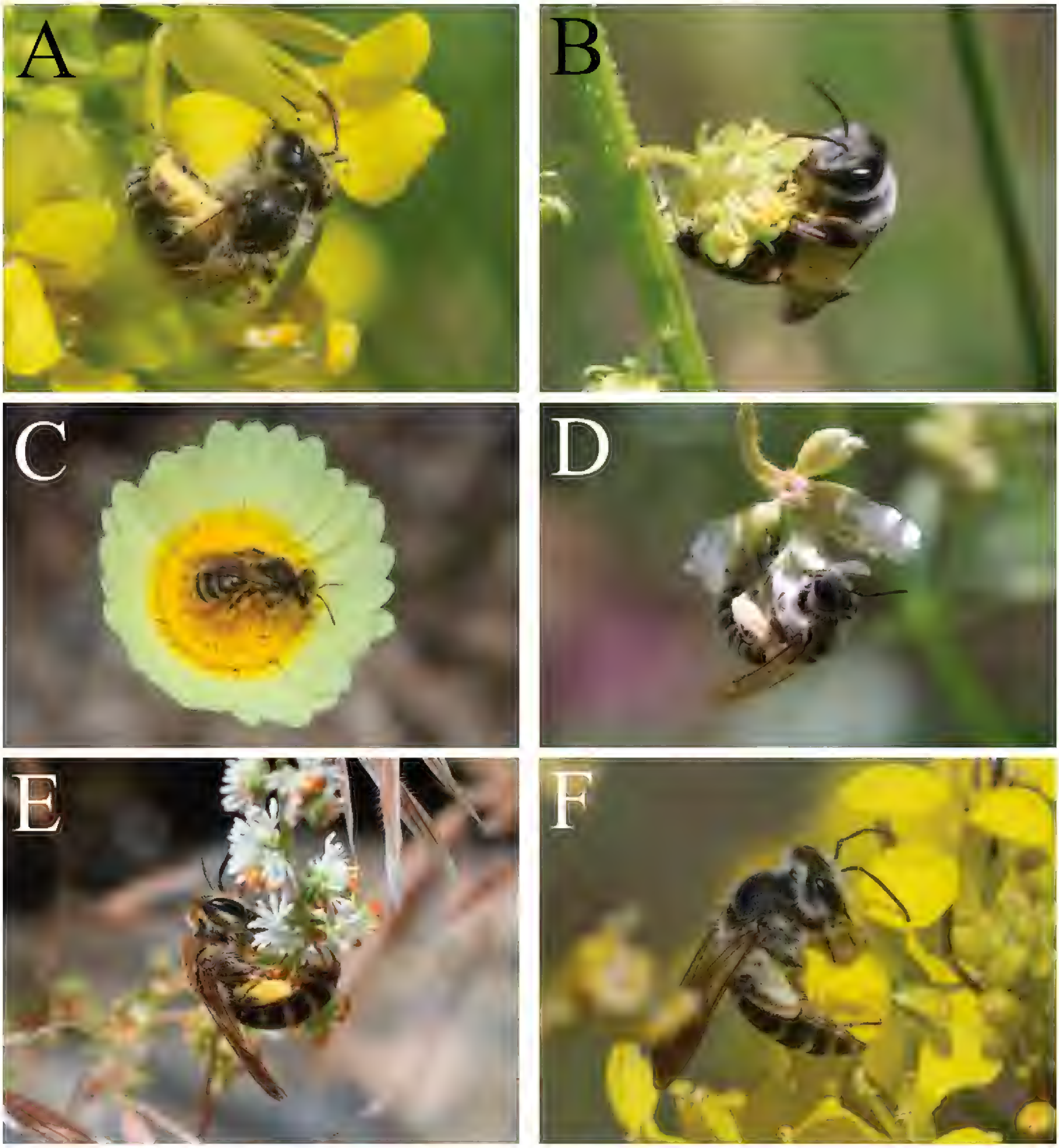

Figure 61. Pollen specialist (oligolectic) *Andrena* species in Iberia **A** *Andrena* (*Notandrena*) *aerinifrons* Dours, 1873 (Brassicaceae) **B** *Andrena* (incertae sedis) *corax* Warncke, 1967 (*Reseda*, Resedaceae) **C** *Andrena* (*Chlorandrena*) *elata* Warncke, 1975 (Asteroideae, Asteraceae) **D** *Andrena* (*Ovandrena*) *farinosa* Pérez, 1895 (*Lotus dorycnium*, Fabaceae) **E** *Andrena* (*Ovandrena*) *oviventris* Pérez, 1895 (*Reseda*, Resedaceae) **F** *Andrena* (*Simandrena*) *vetula* Lepeletier, 1841 (Brassicaceae).

whereas *A. leucophaea* was associated with *Bellis* (Asteraceae; Asteroideae) and may be oligolectic on this subfamily. Both species fly early in the year (typically February-April) and are uncommon in collections; more study is required, but neither species is likely to be specialised on Brassicaceae.

Members of the *relata*-group appear to be specialised on *Reseda* (Resedaceae), including *A. corax* (Fig. 61B). Based on direct observations, all five Iberian members

of the *relata*-group (including *A. macroptera* and *A. murana*) appear to be narrowly oligolectic on *Reseda*, but additional pollen analysis is necessary for confirmation; this being limited by the scarcity of these species in collections.

All studied members of the subgenus *Chlorandrena* are specialists of Asteraceae. However, the only published associations relate to the subfamily Cichorioideae (e.g. Westrich 1989; Schwenninger 2015). However, three Iberian *Chlorandrena* collect exclusively from Asteraceae subfamily Asteroideae: *A. abrupta*, *A. elata* (Fig. 61C), and *A. leucolippa*. These three species form a clade within the *Chlorandrena* along with *A. boyerella* which is also specialised on Asteraceae subfamily Asteroideae (data to be published in the North African revision). This situation resembles the situation within the genus *Panurgus*, members of which are specialised on Asteraceae but for which members of different lineages within *Panurgus* utilise either Asteroideae or Cichorioideae (Wood et al. 2022b).

Within the newly erected subgenus *Ovandrena*, no clear pattern was seen, as *A. farinosa* is a specialist of small-flowered Fabaceae (Fig. 61D) and *A. oviventris* is a specialist of *Reseda* (Fig. 61E). At the moment, *A. farinosa* must be considered a broad oligolege, as the identity of pollen grains removed from museum specimens cannot be identified to the genus level. In Iberia, all my observations of this species come from *Lotus dorycnium* Linnaeus (=*Dorycnium pentaphyllum* Scopoli), and so the species may be more narrowly specialised on the genus *Lotus*, but this requires additional study.

Within the subgenus *Simandrena*, central and northern European species are well-known to be polylectic (Westrich 1989). In contrast, three West Mediterranean species appear to be oligolectic, *A. vetula* (Fig. 61F) and *A. antigana* Pérez, 1895 on Brassicaceae and potentially *A. rhypara* Pérez, 1895 on *Reseda*. All three species belong to the group of *Simandrena* with a strongly shagreened and almost impunctate scutum that is distributed predominantly across the Mediterranean basin, with the highest diversity in North Africa and the Levant. Further study is required to establish the dietary niche of *A. cilissaeformis* which may be polylectic.

Most studied members of the subgenus *Truncandrena* are specialised on Brassicaceae (Westrich 1989), though this subgenus is species-poor in Central Europe and most taxa are Mediterranean and understudied. In Iberia, *A. doursana*, *A. ferrugineicrus*, and *A. nigropilosa* are also specialised on Brassicaceae. However, *A. villipes* was strongly associated with *Cistus* (Cistaceae) based on pollen analysis and direct observations, a behaviour that has not previously been demonstrated for this subgenus. As discussed above, this is likely to be the dietary niche for *A. ghisbaini*, the two species together appear basally in the COI phylogeny (Fig. 29). Additional study is required to establish whether this basal position is supported by more powerful genetic analyses.

The subgenus *Micrandrena* contains mixture of oligolectic and polylectic species in central and northern Europe, though polylectic species predominate (Westrich 1989). In Iberia, numerous species display oligolectic behaviour, specifically *A. ampla* (Apiaceae), *A. djelfensis* and *A. fabrella* Pérez, 1903 (Cistaceae), *A. longibarbis*, *A. nitidula*, *A. orana*, and *A. tenuistriata* (Brassicaceae), and *A. omnilaevis* (Crassulaceae). The dietary status of *A. spreta* is somewhat unclear, as specimens from both the

spring and summer generations analysed here collected predominantly Brassicaceae pollen (93.1%). There is a bias towards spring generation specimens which are typically more abundant, and which fly at a time of year with high Brassicaceae availability. Additional samples from the summer generation are required, but the species can provisionally be considered to be polylectic with a strong preference for Brassicaceae.

There was one species for which the empirical data slightly conflicts with what I believe to be the true dietary niche. For *A.* (*Avandrena*) *panurgina*, the pollen results showed that 93.6% of collected pollen came from Geraniaceae, with the remaining pollen from Asteraceae and Brassicaceae. Following the criteria of Müller and Kuhlmann (2008), this species would not necessarily be classified as oligolectic on Geraniaceae. However, Geraniaceae pollen grains are very large, usually in excess of 50 μm, and it is possible for contaminant pollen to be present between these large grains in a way that is much less common when dealing with smaller grains which pack into scopal hairs more tightly. Behavioural observations of *A. panurgina*, including those of males which patrol around *Erodium* (Geraniaceae) plants in March and early April, strongly suggests oligolecty on Geraniaceae. All behavioural pollen-foraging observations of *A. panurgina*, along with other western *Avandrena* Warncke, 1968 species *A. avara*, *A. erodiorum*, and *A. melacana* Warncke, 1967 have been made at *Erodium* (Wood and Ortiz-Sánchez 2022; pers. obs., Álvarez Fidalgo in litt.). Consequently, the presence of Asteraceae and Brassicaceae pollen in the quantitative analysis is considered likely to be contamination, and *A. panurgina* is considered to be an oligolege of Geraniaceae along with the other western *Avandrena* species (see Pisanty et al. 2022a).

The data presented here also resolve the pollen collection preferences of the West Mediterranean *A.* (*Rufandrena*) *orbitalis* Morawitz, 1871 and *A.* (*Rufandrena*) *rufiventris* Lepeletier, 1841 which belong to the subgenus *Rufandrena* Warncke, 1968 that may contain three species, with a further species known from Syria and Hatay province in Turkey (Wood 2023b) which requires genetic confirmation of its placement. The two West Mediterranean species are instantly recognisable in the female sex because of their extraordinarily long and incredibly plumose hairs of the tibial and femoral scopae and both flocculi (see Fig. 64H). Baldock et al. (2018) identified the use of *Plantago* (Plantaginaceae) pollen by *A. orbitalis*, but did not come to a firm conclusion as to the overall dietary niche of this species. Analysis of scopal pollen loads and behavioural observations (*A. orbitalis* in the Algarve, Portugal and *A. rufiventris* in the Middle Atlas, Morocco) show that both *A. orbitalis* and *A. rufiventris* are specialists of *Plantago*. In the spring, usually in the months of March and April, both species can be seen visiting low-growing *Plantago* species. Upon arriving (Fig. 62C) at a small flower head, they grab onto its side and present the underside of their body so that falling grains will land on their venter and scopae (Fig. 62A). They will then manipulate the anthers using their fore legs and mandibles (Fig. 62D), often directly scraping pollen from the anthers using their mandibles (Fig. 62E). When the flower head is long, they will sometimes work from bottom to top, often vigorously dislodging pollen grains that can form a small but distinctly visible cloud (Fig. 62B). Pollen landing on the body is then groomed into the scopae.

As *Plantago* is wind-pollinated, it does not provide a nectar source. Nectar is therefore collected from other plants such as *Crepis* (Asteraceae), *Malva* (Malvaceae, Álvarez Fidalgo in litt.), or *Reseda* (Fig. 62F). Pollen is packed into the scopae dry, and inspection of freshly caught and pinned specimens shows that pollen rapidly falls out of the scopae with gentle manipulation, for example with an entomological pin. This

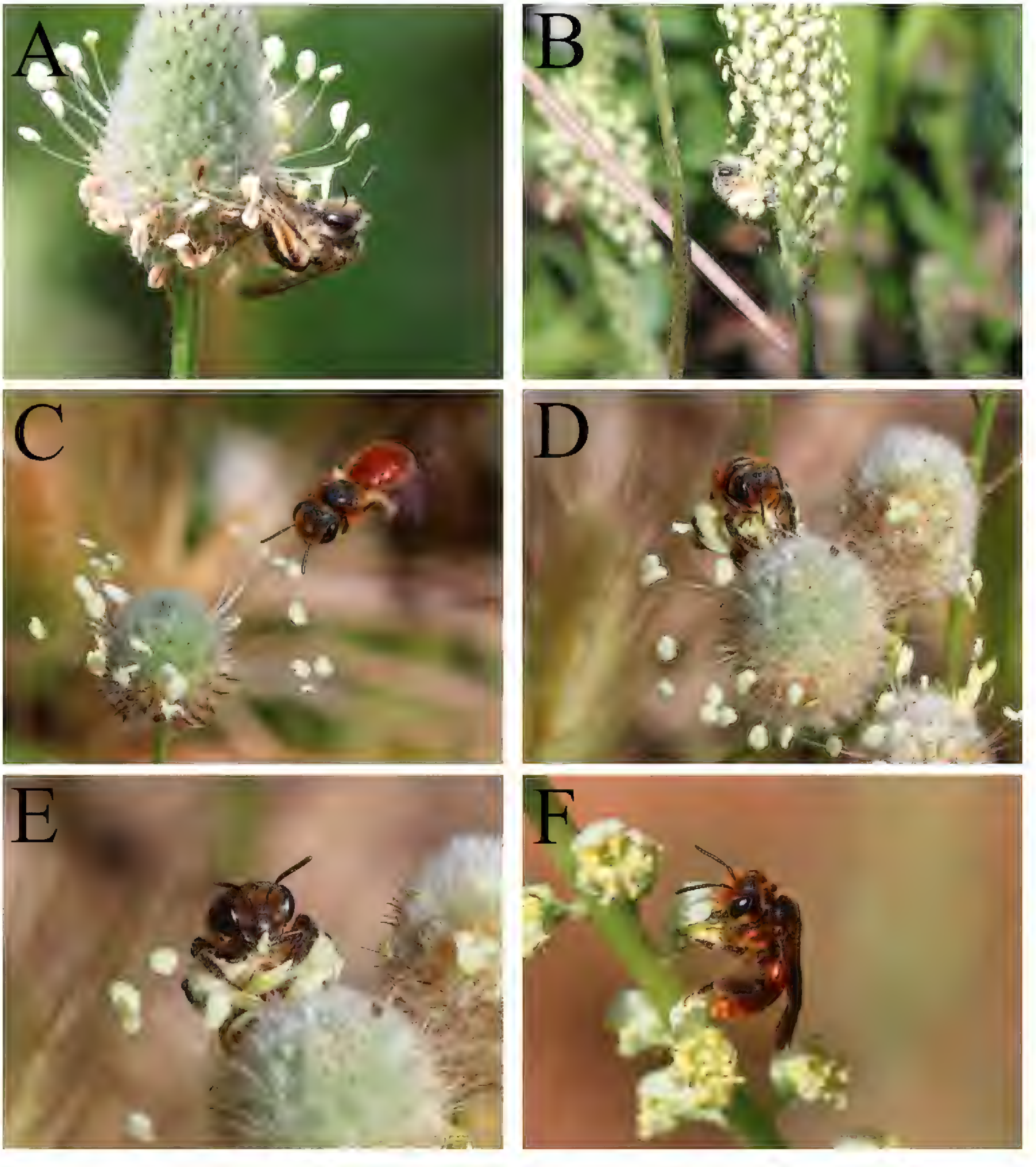

Figure 62. Use of *Plantago* (Plantaginaceae) pollen by *Rufandrena* Warncke, 1968 species. *Andrena* (*Rufandrena*) *orbitalis* Morawitz, 1871 **A** female, manipulating *Plantago* anther **B** female, vigorously collecting *Plantago* pollen; *Andrena* (*Rufandrena*) *rufiventris* Lepeletier, 1841 **C** female approaching *Plantago* flower head **D** female manipulating *Plantago* anthers with forelegs and mandibles **E** female scraping pollen from *Plantago* anther using mandibles **F** female drinking nectar at *Reseda* (Resedaceae) with empty scopae.

probably explains both why the scopal hairs are so densely and finely plumose in order to retain these small pollen grains (typically <20 μm in diameter), and also why very few specimens in museum collections have scopae that retain pollen, as dry grains are easily dislodged after specimen collection. Use of pollen from wind-pollinated plants is well-known in bees, predominantly by social polylectic species (Saunders 2018), but also by solitary species, including species belonging to genera such as *Lipotriches* Gerstaecker, 1858 (Halictidae) that can be oligolectic upon members of the Poaceae (Immelman and Eardley 2000). Whilst some *Andrena* species are known to collect pollen from wind-pollinated plants (Wood and Roberts 2017; Saunders 2018), to my knowledge this is the first time that any *Andrena* species has been demonstrated to be specialised for pollen collection on a wind-pollinated plant.

Finally, a note on the pollen collection preferences of *A. afzeliella* and *A. ovatula* is beneficial. Praz et al. (2022) demonstrated that *A. afzeliella* is polylectic with a strong preference for Fabaceae, and *A. ovatula* is oligolectic on Fabaceae. Additional detail and context can be provided based on observations in Iberia which help to explain their differing distributions and ecologies. *Andrena afzeliella* typically visits herbaceous Fabaceae, such as *Trifolium pratense*. It visits honestly, and does not manipulate the flowers beyond what is typically expected in an 'honest' visit. It can be found commonly on the open steppe habitats of Old Castile, for example in Segovia, Castroserna de Abajo, Buitreras y Cuevas (25.vii.2021, Fig. 63A, B). In contrast, *A. ovatula* prefers areas with an Atlantic influence that host members of the tribe Genisteae (Fabaceae), usually woody species (e.g. *Cytisus*, *Genista*, *Ulex*, etc.). Here it visits these flowers honestly for nectar, but roughly manipulates the petals with its two front pairs of legs and its mandibles in order to access the anthers. This can be seen in western and north-western Iberia, as well as in the Sistema Central such as at Segovia, Riofrío de Riaza, Embalse de Riofrío (27.vii.2021, Fig. 63C–F). In my experience, I have never observed *A. afzeliella* manipulating Fabaceae flowers like this. The relationship with woody Genisteae may explain the earlier emergence of the first generation of *A. ovatula* (peaking April compared to May for *A. afzeliella*; see typical emergence patterns in north-western Europe in Praz et al. 2022) due to the earlier flowering of woody Fabaceae relative to herbaceous Fabaceae. Consequently, *A. ovatula* is typically not encountered in open steppe habitats, whereas *A. afzeliella* typically avoids western parts of Iberia with a strong Atlantic influence.

Pollen use by bivoltine species

A widespread behaviour within *Andrena* is bivoltinism, i.e. species producing a spring and a summer generation. For several bivoltine species, their dietary niche is not yet clear. There is a lack of clarity over two species within *Aenandrena*. For the 15 pollen loads of *A. aeneiventris* (collected between 11th June and 25th July) and the 22 pollen loads of *A. hedikae* (collected between 21st May and 25th July), each load was comprised entirely of Apiaceae pollen. However, both species are bivoltine, and pollen loads from the spring generation must be analysed. Osytshnjuk et al. (2005) state that both species visit Brassicaceae in the spring generation, and Kocourek (1966) gives a

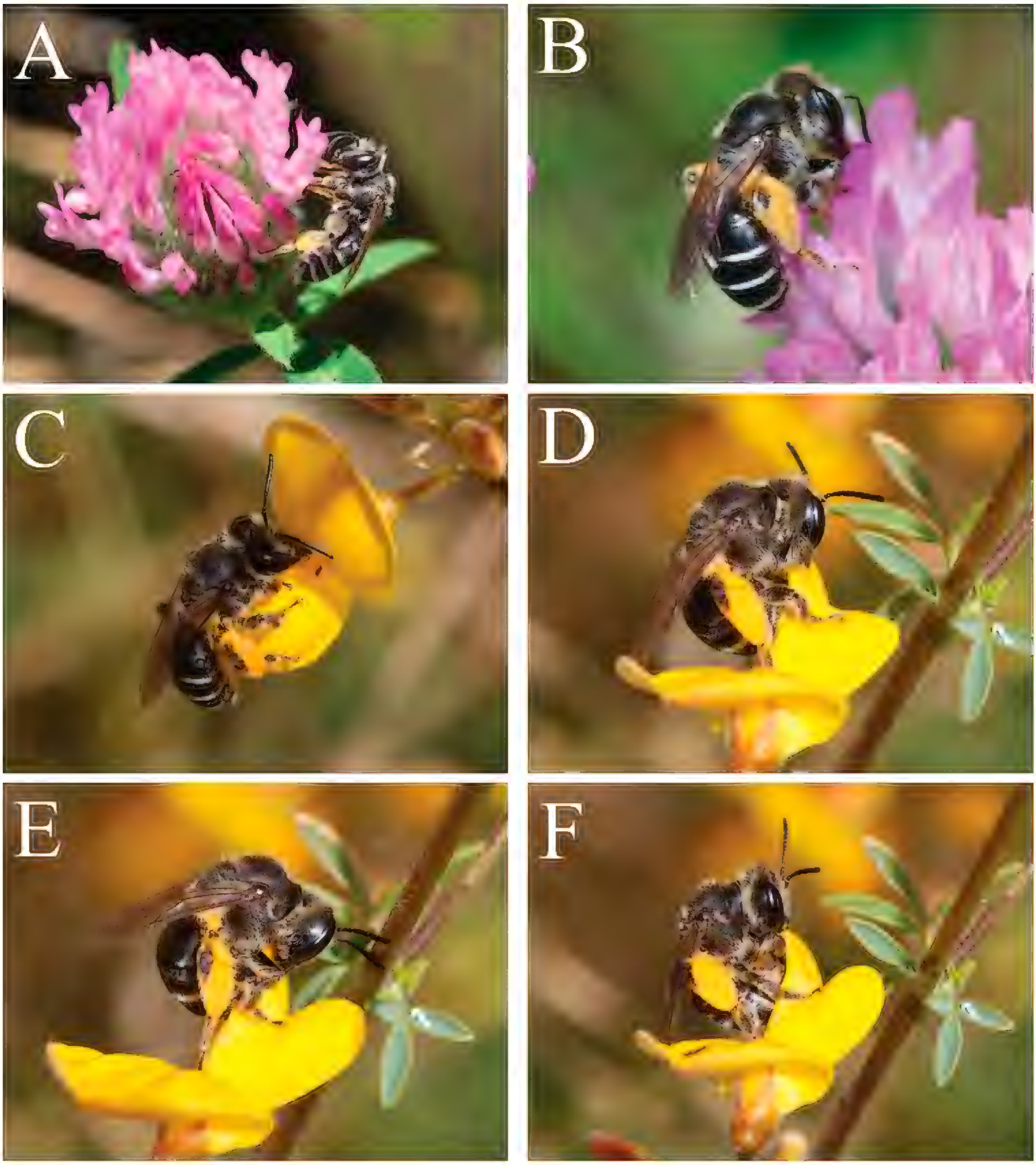

Figure 63. *Andrena* (*Taeniandrena*) *afzeliella* (Kirby, 1802) **A, B** foraging female at *Trifolium pratense* (Fabaceae); *Andrena* (*Taeniandrena*) *ovatula* (Kirby, 1802) **C–F** foraging female at Genistae spp. (Fabaceae).

list of several Brassicaceae species along with *Sedum* (Crassulaceae) and *Euphorbia* (Euphorbiaceae). I have personally never observed *A. aeneiventris* at flowers of Brassicaceae in the West Mediterranean despite extensively searching this botanical family during the Iberian spring for the large number of univoltine species that specialise on this family. However, in an Iberian context, both species are quite uncommonly observed and collected in their first generation, certainly compared to their abundance in the summer. More study is required, and neither species should be classified as oligolectic on Apiaceae until more pollen load data are available, ideally also from other parts of

southern to south-central Europe. A similar problem is found within the subgenus *Brachyandrena* Pittioni, 1948. Very few pollen loads were available for analysis, but both *A. colletiformis* and *A. miegiella* Dours, 1873 were found to only collect Apiaceae pollen. Both species are also bivoltine. Osytshnjuk et al. (2005) state that *A. colletiformis* visits a variety of botanical families, but prefers the Apiaceae. In this dataset, pollen bearing-specimens of *A. colletiformis* were collected between 25th April and 20th July, thus encompassing both generations. More study is required to establish if pollen sources other than Apiaceae are utilised. Based on observations, they are almost exclusively found on Apiaceae and can be provisionally considered oligolectic on this family.

In contrast, *A. verticalis* provides an example of a bivoltine species that uses Apiaceae, but not exclusively. *Andrena verticalis* flies between March and August, and in this dataset collects 56.3% of its pollen from Brassicaceae (mostly in the spring) and 43.8% of its pollen from Apiaceae (mostly in the summer). However, the use of specific botanical families is not restricted to the two generations, and instead is based on local availability. Interestingly, no mixed pollen loads were detected in the 30 pollen loads examined here, each consisting only of a single botanical family. This recurring pattern of Apiaceae and Brassicaceae use within bivoltine species can be seen for *A. hypopolia*, which also displays mesolecty on these two families. Additional study is required across these aforementioned species to robustly test the limits of mesolecty on Apiaceae and Brassicaceae across two generations (*A. verticalis* and *A. hypopolia*), oligolecty on Apiaceae in both generations (possibly *A. colletiformis* and *A. miegiella*), and possible oligolecty in each generation but upon a different botanical family (potentially *A. aeneiventris* and *A. hedikae*).

Finally, it is necessary to discuss the case of *A. mucida* which appears to be differentially oligolectic in its spring and summer generation. The terminology surrounding pollen use in bees has been refined and categorised several times in recent years (Cane and Sipes 2006; Müller and Kuhlmann 2008; Kuhlmann and Timmermann 2011; Cane 2020), with debate over how broad or how narrow to make the existing categories. However, to my knowledge, no examples of bee species displaying different specialisation in different generations has been provided or discussed, much less this behaviour formally named. Kocourek (1966) noted the differential foraging behaviour of *A. mucida*, stating that the 1st generation visited *Salix* and *Muscari*, with the 2nd generation visiting *Scabiosa*. Unlike the case in some bivoltine *Andrena* species that may display differential levels of specialisation between generations but which cannot unambiguously be assigned to a specific generation morphologically (e.g. some *Micrandrena*), *A. mucida* displays simple tibial scopal hairs in the spring generation, and plumose tibial scopal hairs in the summer generation. Individuals can therefore be assigned to each generation with confidence (rather than based only on collection date), and when combined with pollen analysis the data confirm this differential pollen collection behaviour. Therefore, is *A. mucida* simply a polylectic species, or rather differentially oligolectic? Given the possibly unique nature of this behaviour, it would be beneficial to formally name this pattern of pollen collection *heterolecty*, in which a species is i) bivoltine, ii) oligolectic in both generations,

and iii) each generation is oligolectic on different botanical families. This name will highlight this highly unusual behaviour, rather than have it hidden away under an all-encompassing 'polylecty'.

Summary for pollen use by Iberian *Andrena* species

For the 75 Iberian species (not including *A. rufiventris*) for which pollen data are presented, the majority are oligolectic or assessed as likely to be oligolectic. Excluding species for which insufficient data are available to allow confident classification (*A. aeneiventris*, *A. colletiformis*, *A. hedikae*, and *A. miegiella*), 49 species are classified as oligolectic, 21 as polylectic, and one (*A. mucida*) as heterolectic. This high proportion of oligolectic species, most of which have their pollen preferences demonstrated here for the first time, illustrates the degree to which the Iberian fauna i) hosts many specialised species and ii) has been chronically understudied with regard to the basic biology of its constituent bee species. Within the oligolectic species studied here, there is a clear preference for Brassicaceae, this family hosting 22 species, followed by Asteraceae (n=10), Resedaceae (n=6), Cistaceae (n=3), Geraniaceae (n=3), Apiaceae (n=2), and Crassulaceae, Fabaceae, and Plantaginaceae (n=1 each). The broader faunal trends shown by Iberian *Andrena* species will be examined in detail in a subsequent publication.

Identification key

The males of *A. cilissaeformis*, *A. erodiorum*, *A. foeniculae*, *A. juliae*, *A. macroptera*, *A.* aff *mica*, *A. ortizi*, *A. tenostra*, and *A. urdula* are currently unknown, so they are not included in the key; a level of caution must therefore be taken when working with morphologically similar species. The Spanish *A. allosa* Warncke, 1975 is unknown to me, so the relevant couplet is based on material from the Alps (see Praz et al. 2019).

Unfortunately, after consideration, I have also decided to exclude the male of *A. exigua* from the key because its confident determination is not clear to me. Existing literature (Gusenleitner and Schwarz 2002; Dardón et al. 2014) is light on detail, and my own examination of extremely limited material has not cemented the concept. Due to the nominal rarity of this taxon, no material was available for genetic study, further limiting the confidence with which the sexes can be associated. Confident sex association and determination of *A. exigua* males must remain an open question for students of the Iberian fauna.

For supplementary illustrations, please consult the works cited in the Methodology, particularly Schmid-Egger and Scheuchl (1997) for Euro-Siberian species, as well as my publications describing Iberian species. Moreover, in the near future, the ongoing ORBIT project (providing taxonomic resources for European bees, https://orbit-project.eu/) will provide images for all European *Andrena* species. Between this key and the images presented there, confident determination should be possible in the majority of cases.

The female and male keys are separated for convenience. For the female key, the following shortcuts can be used:

A. Posterior face of hind femur with latitudinal row of spines or teeth....... **go to 2**
B. Hind tibial spur clearly broadened, either at its base or submedially. Large to very large species, at least 12 mm in length .... **go to 25**
C. Hairs of the tibial scopae clearly plumose .... **go to 42**
D. Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate .... **go to 51**
E. Scutum and scutellum with squamous hairs .... **go to 55**
F. Viewed laterally, propodeal corbicula with internal surface (lateral faces of the propodeum) glabrous AND propodeal corbiculae complete (possessing both a dorsal and anterior fringe (subgenus *Simandrena*) .... **go to 64**
G. Fovea strongly constricted medially, strongly diverging from the inner margin of the compound eye dorsally (former subgenus *Hyperandrena*)............... **go to 75**
H. At least some tergal discs extensively red-marked................................ **go to 77**
I. Head, mesosoma, or tergal discs with metallic reflections (note, *A. nigroaenea* (Kirby) can have bronzy reflections on the terga; if the tibial scopa is composed at least partly of orange-red hairs, go to 205)....................................... **go to 84**
J. Small black species, body length under 8 mm, or if up to 10 mm then with lateral faces of the propodeum with clear pattern of raised star-shaped wrinkles (all members of the subgenera *Aciandrena*, *Graecandrena*, *Micrandrena*) ...... **go to 92**
K. Clypeus flattened over majority of its surface (subgenus *Taeniandrena*) ...**go to 139**
L. Fovea dorsally narrow, occupying at most ⅓ of space between lateral ocellus and compound eye, ventrally narrowing strongly (subgenus *Euandrena*)....... **go to 152**
M. Clypeus punctate, interspaces forming weakly raised longitudinal wrinkles (former subgenus *Zonandrena*).. **go to 163**
N. Dorsolateral surface of the propodeum reticulate, with large and shallow punctures, clearly contrasting the shagreened and shiny propodeal triangle, this lacking lateral carinae and becoming shinier on the declivity (subgenus *Hoplandrena*)....**go to 168**
O. Pronotum laterally keeled, angulate, keel runs up dorsally to an angled corner. .... **go to 174**
P. Large species (over 12 mm in length). Typically with abundant black, brown, and/or white pubescence. Clypeus strongly domed. Ocelloccipital distance long, at least 2 times the diameter of a lateral ocellus (subgenus *Melandrena partim*) ....**go to 206**
Q. Without this combination of characters; remaining species .... **go to 212**

Females

1 Posterior face of hind femur with latitudinal row of spines or teeth (Fig. 64A, B). Note, if there is also a developed latitudinal carina, then the spines can be difficult to see (subgenus *Lepidandrena*, these species with squamous hairs on the scutum and scutellum) **2**
– Posterior face of hind femur without latitudinal row of spines or teeth. A latitudinal carina may be present (e.g. *Andrena flavipes*) **24**

2 Mesonotum dorsally with short squamous hairs (Fig. 64C, D) **3**

– Mesonotum with longer hairs, these never squamous.................................. **9**

3 At least the disc of T2 red-marked **4**

– All terga dark... **5**

4 Metasoma entirely red-marked; mesonotum with squamous hairs black. Widespread throughout Iberia, associated with *Asphodelus* (Asphodelaceae)... ***sardoa* Lepeletier**

– Metasoma with red markings typically restricted to T2–3; mesonotum with squamous hairs brown-grey. Restricted to the Pyrenees, associated with *Campanula* (Campanulaceae) .... ***rufizona* Imhoff**

5 T1 comparatively sparsely punctate, large punctures separated by >1 puncture diameter, with scattered micropunctures between these large and relatively coarse punctures. Foveae with outer margin clearly defined, foveae depressed, separated from lateral ocellus by a distance subequal to its diameter (Fig. 64E) .... ***leucolippa* Pérez**

– T1 finely and densely punctate, punctures separated at most by 1 puncture diameter, usually by 0.5 puncture diameters, without micropunctures. Foveae with outer margin poorly defined, foveae not clearly depressed, separated from lateral ocellus by a distance greater than its diameter (Fig. 64F) **6**

6 Galea shagreened and dull, clypeus also shagreened and dull with clear impunctate longitudinal midline. Hind tibiae orange. Associated with *Ornithogalum* (Asparagaceae) .... ***baetica* Wood**

– Galea smooth and shiny, clypeus also at least partially shiny, without impunctate longitudinal midline. Hind tibiae dark. Associated with *Campanula* (Campanulaceae) 7

7 Tarsal segment 5 of the hind leg elongate and strongly bent. Squamous hairs light brown. Larger, 13–14 mm .... ***curvungula* Thomson**

– Tarsal segment 5 of the hind leg shorter, at most as long as the two preceding segments taken together, only weakly bent. Squamous hairs darker grey brown. Somewhat smaller, not larger than 12 mm.................................. **8**

8 Squamous hairs very thick, in fresh specimens the underlying scutal punctures are obscured. Midline of the scutum is only slightly impressed. Process of labrum markedly elongate with a clear apical emargination in the fore margin. Larger, 10–12 mm .... ***pandellei* Pérez**

– Squamous hairs moderately thick, the underlying scutal punctures clearly visible. Midline of the scutum clearly impressed. Process of labrum regularly trapezoidal, not elongate, fore margin almost straight. Smaller, 8–10 mm .... ***paucisquama* Noskiewicz**

9 Tibial scopae composed predominantly of simple hairs, at most with occasional and scattered plumose hairs (Fig. 64G) **10**

– Tibial scopae extensively composed of plumose hairs (Fig. 64H) **13**

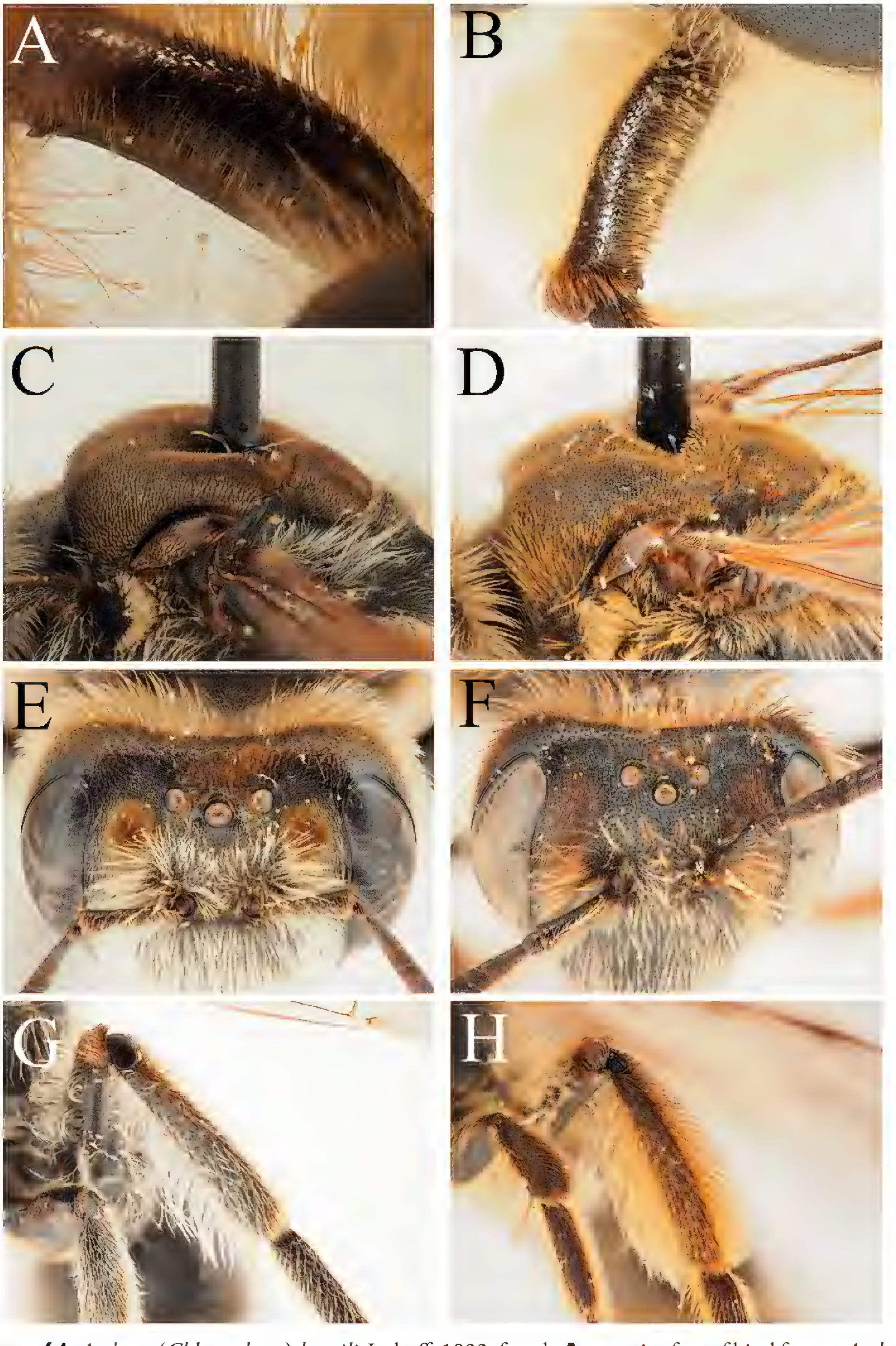

Figure 64. *Andrena* (*Chlorandrena*) *humilis* Imhoff, 1832, female **A** posterior face of hind femur; *Andrena* (*Rufandrena*) *orbitalis* Morawitz, 1871, female **B** posterior face of hind femur **H** tibial scopa, profile view; *Andrena* (*Lepidandrena*) *pandellei* Pérez, 1895, female **C** scutum, profile view; *Andrena* (*Chlorandrena*) *leucolippa* Pérez, 1895, female **D** scutum, profile view **E** foveae, dorsal view; *Andrena* (*Lepidandrena*) *curvungula* Thomson, 1870, female **F** foveae, dorsal view; *Andrena* (*Cryptandrena*) *ventricosa* Dours, 1873, female **G** tibial scopa, profile view.

10 Propodeal triangle poorly defined, without lateral carinae, smooth and with granular shagreen, more or less shiny over the majority of its area. Larger, 9–10 mm.. ***monilia* Warncke**

– Propodeal triangle shagreened and dull or with clearly raised carinae laterally and medially. Smaller, length never exceeding 8 mm **11**

11 Terga strongly and densely punctate, punctures separated by 0.5 puncture diameters, underlying surface smooth and shiny. Propodeal triangle clearly delineated laterally by strongly raised carinae .... ***ventricosa* Dours**

– Terga shagreened and matt, with obscure and shallow punctures. Propodeal triangle lacking lateral raised carinae, poorly defined...............................**12**

12 Process of the labrum narrow, clearly produced into a narrow, apically pointed triangle. Head and mesosoma with black pubescence..................... ....***panurgina* De Steffani**

– Process of the labrum broad, clearly at least three times broader than long. Head and mesosoma with brownish to greyish-white pubescence .... ***avara* Warncke aggregate** (potentially including multiple valid species)

13 Scutum and scutellum with clear longitudinal striations........***rhyssonota* Pérez**

– Scutum and scutellum without longitudinal striations **14**

14 Fovea with inner margin clearly dorsally diverging from the inner margin of the compound eye, curved towards the lateral ocellus (*livens*-group)...........**15**

– Fovea with inner margin not dorsally diverging from the inner margin of the compound eye, not noticeably curved towards the lateral ocellus **17**

15 Terga with weak but clear metallic green-blue reflections. Antennae usually ventrally dark, at most obscurely lightened dark brown. Process of the labrum trapezoidal, small, only lightly broader than long............***nigroolivacea* Dours**

– Terga dark, without any metallic reflections. Antennae usually extensively lightened orange ventrally. Process of the labrum broader, at least two times wider than long...**16**

16 Discs of T2–3 at their bases consistently and densely punctate, punctures typically separated by 1 puncture diameter, at most by 2 puncture diameters. Distributed throughout Iberia .... ***livens* Pérez**

– Discs of T2–3 at their bases more sparsely punctate, punctures separated by more than 3 puncture diameters. Rare, known only from a single specimen captured near Madrid ....***agnata* Warncke**

17 Foveae strongly constricted ventrally, here narrower than the width of a flagellum (*taraxaci*-group)..**18**

– Foveae not strongly constricted ventrally, more or less as wide as dorsally, not narrower than the width of a flagellum **20**

18 Scutum medially with greatly reduced shagreenation, here more or less smooth and shiny. Facial pubescence relatively dark, with black to dark brown hairs along the inner margins of the compound eyes. Rare, southern and south-eastern Spain only .... ***curtivalvis* Morice**

– Scutum shagreened, uniformly dull across its entire surface. Facial pubescence bright, with at most scattered dark hairs. Throughout Iberia **19**

19 Depressions of terga, especially T3–4, extensively lightened orange-yellow, semi-transparent. Discs of T2–3 densely punctate, punctures with strongly raised rims .... ***senecionis*** **Pérez**

– Depressions of terga at most with apical rim narrowly lightened orange-yellow. Discs of terga weakly and relatively obscurely punctate, puncture rims weakly raised..***rhenana*** **Stöckhert**

20 Tergal margins entirely lightened whitish-yellow hyaline. Face (particularly vertex), scutum, and scutellum with subtle metallic blue-green reflections **21**

– Tergal margins never entirely lightened, at most narrowly lightened yellow hyaline. Face (particularly vertex), scutum, and scutellum dark, without metallic reflections...**22**

21 Found in dry to steppic areas in central Spain. Scutum with clear punctures that are visible against the strong background shagreenation. Scutellum with shiny interspaces between punctures[3] ....***elata*** **Warncke**

– Found in areas close to or on the coast in southern Portugal and Spain. Scutum with obscure punctures that disappear into the strong background shagreenation. Scutellum with interspaces shagreened[3] .... ***abrupta*** **Warncke**

22 T2–4 depressed at their base, marginal areas of T2–4 with apical white hair bands that obscure the underlying surface in fresh specimens. Posterior face of the hind femur with long spines ....***orbitalis*** **Morawitz**

– T2–4 not depressed basally, apically with marginal areas with at most scattered orange-yellow hairs, these not forming distinct bands which obscure the underlying surface. Posterior face of the hind femur with short teeth......................**23**

23 T2 between the punctures weakly shagreened, comparatively shiny. Larger species, over 10 mm. Found in more temperate parts of Iberia, generally absent in hot Mediterranean habitats[4].................................***humilis*** **Imhoff**

– T2 between the punctures strongly shagreened and dull. Smaller species, under 10 mm. Found in hotter parts of Iberia, the dominant taxon in Mediterranean habitats[4] .... ***cinerea*** **Brullé**

24 (1) Hind tibial spur clearly broadened, either at its base (Fig. 65A) or submedially (Fig. 65B). Large to very large species, at least 12 mm in length **25**

– Hind tibial spur not broadened at its base or submedially, more or less parallel-sided. Size variable...**41**

25 Propodeum dorsolaterally with dense punctures, punctures separated by <1 puncture diameter (Fig. 65C). Propodeum rounded in profile view, without clearly separated horizontal and vertical parts (subgenus *Holandrena* Pérez)...**26**

– Propodeum dorsolaterally with raised reticulation or rugosity (Fig. 65D), without dense punctures or without punctures at all. Propodeum with separated horizontal and vertical parts **29**

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3 These two species are challenging to separate in the female sex; geographical context cues and association with the more distinctive males should be used.

4 These two species are challenging to separate in the female sex. Association with the more distinctive males should be made.

26 Vertex wide, ocelloccipital distance at least as wide as three times the diameter of a lateral ocellus..***variabilis* Smith**

– Vertex narrower, ocelloccipital distance never as wide as three times the diameter of a lateral ocellus...**27**

27 Disc of T1 densely punctate, punctures typically separated by 1 puncture diameter. Scutellum dull between punctures. Tergal hair bands interrupted medially..***labialis* (Kirby)**

– Disc of T1 more sparsely punctate, punctures separated by greater than 1 puncture diameter, typically by 2 puncture diameters. Scutellum shiny between punctures. Tergal hair bands complete in fresh specimens.............**28**

28 Flying in the spring (April–May). Terminal fringe dark blackish-brown. Ocelloccipital distance narrower, 1 times the diameter of a lateral ocellus[5].. ....***flavilabris* Schenck**

– Flying in the summer (July–August). Terminal fringe light. Ocelloccipital distance wider, 1–1.5 times the diameter of a lateral ocellus[5] ... ***decipiens* Schenck**

29 Hind tibial spur broadened submedially. Propodeal triangle simply defined laterally by weak and obscurely raised carinae, internal surface without a dense network of strongly raised honeycomb-like rugosity. Terga often red-marked. Exclusively summer flying species, from May onwards.............**30**

– Hind tibial spur broadened at its base. Propodeal triangle clearly defined laterally by strongly raised carinae (Fig. 65D), internal surface with dense network of strongly raised honeycomb-like rugosity (though this can be weak in members of the subgenus *Suandrena* Warncke). Tergal only very rarely red-marked. Flying in the spring or summer **31**

30 Tibial scopa ventrally composed of long plumose hairs. Posterior face of the hind femora with clear latitudinal carina. Terga usually red marked, though an entirely melanic form can be found in south-eastern Spain (ssp. *nigricauda* Wood). Associated with scabious (former Dipsacaceae = Caprifoliaceae). Restricted to montane grasslands in northern and central Spain with isolated populations in the Sierra de Cazorla and Sierra Nevada.... ***hattorfiana* (Fabricius)**

– Tibial scopa simple or with at most occasional obscurely plumose hairs. Posterior face of the hind femora without a latitudinal carina. Terga never red-marked. Associated with yellow Cichorioideae (Asteraceae). Restricted to the Pyrenees and Cantabrian Mountains ....***polita* Smith**

31 Terminal fringe dark medially and white laterally (Fig. 24D, F). Lateral faces of the propodeum with strongly pronounced network of coarse ridges and creases..**32**

– Terminal fringe uniformly dark. Lateral faces of the propodeum without ridges, either unsculptured or at most with individually raised points which do not joint together to form a network **34**

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5 These two species can be challenging to separate. Association with males should be made, along with phenological context.

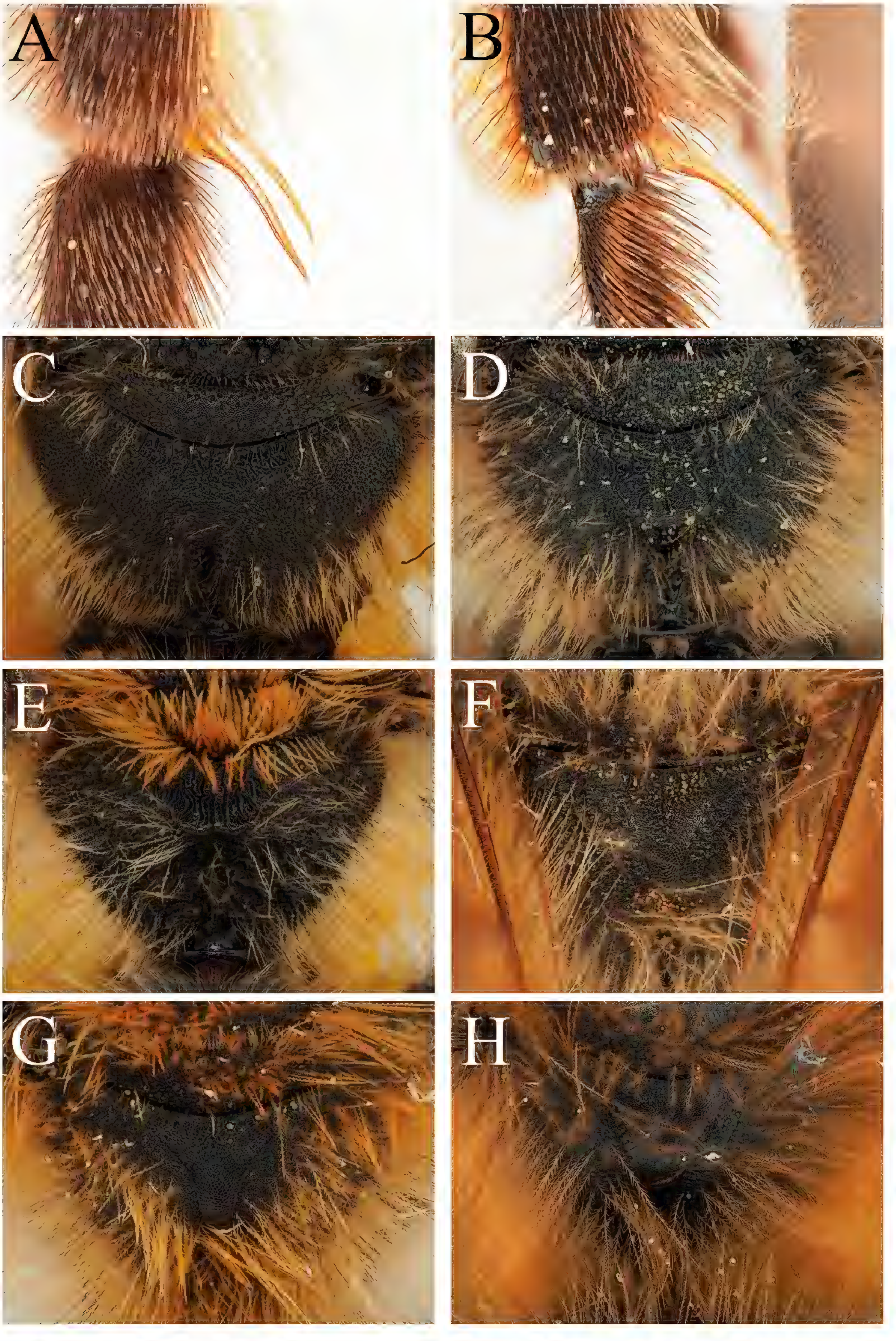

Figure 65. *Andrena* (*Plastandrena*) *bimaculata* (Kirby, 1802), female **A** hind tibial spurs, dorsal view **D** propodeum, dorsal view; *Andrena* (*Holandrena*) *labialis* (Kirby, 1802), female **B** hind tibial spurs, dorsal view **C** propodeum, dorsal view; *Andrena* (*Trachandrena*) *haemorrhoa* (Fabricius, 1781), female **E** propodeum, dorsal view; *Andrena* (*Melandrena*) *nigroaenea* (Kirby, 1802), female **F** propodeum, dorsal view; *Andrena* (*Andrena*) *helvola* (Linnaeus, 1758), female **G** propodeum, dorsal view; *Andrena* (*Hoplandrena*) *scotica* Perkins, 1916, female **H** propodeum, dorsal view.

32 Disc of T1 strongly and densely punctate, punctures separated by <1 puncture diameter .... ***asperrima* Pérez**
– Disc of T1 with sparse punctate, punctures on average separated by 2 puncture diameters **33**
33 Metasoma with metallic blue reflections. T4 laterally with thick white hair patches. Pygidial plate narrow, laterally with a shiny depressed marginal area .... ***agilissima* Scopoli**
– Metasoma black, without metallic blue reflections. T4 laterally with only loose white hair, not forming dense hair patches. Pygidial plate broad, flat, without a depressed and shiny marginal area .... ***afrensis* Warncke**
34 Terga with metallic blue-green reflections. Mesepisternum and dorsolateral faces of the propodeum more or less smooth, granularly shagreened, weakly and obscurely punctate (subgenus *Suandrena*) **35**
– Terga black or red-marked, but never with metallic reflections. Mesepisternum and dorsolateral faces of the propodeum with dense network of raised rugosity **37**
35 Propodeal triangle weakly defined, internal rugosity fine and obscure. Known only from Cádiz province, flying in December .... ***gades* Wood & Ortiz-Sánchez**
– Propodeal triangle strongly defined, with pronounced internal rugosity. More widespread across Iberia **36**
36 Process of the labrum triangular with clear apical point. Throughout Iberia[6] .... ***suerinensis* Friese**
– Process of the labrum broadly triangular with apical margin truncate. Confirmed males known only from central, eastern, and south-eastern Spain[6]... .... ***cyanomicans* Pérez**
37 Pronotum laterally with strong humeral angle. Terga with extremely fine punctation, punctures minute, separated by <0.5 puncture diameters......... .... ***fuscosa* Erichson**
– Pronotum laterally rounded, without humeral angle. Terga with much coarser punctation, punctures separated by >1 puncture diameter **38**
38 Pubescence of body predominantly black, tibial scopa predominantly composed of white hairs **39**
– Pubescence of body variable, but usually with extensive brown hairs on mesosoma; tibial scopa usually orange, never predominantly composed of white hairs **40**

6 These two species cannot be adequately separated in the female sex. Warncke's unpublished key gave this character, but I am not convinced that it is robust. Association must be made with the distinctive males.

39 Bivoltine (typically March–April and July–August). Common and widely distributed throughout Iberia[7] .... ***pilipes*** **Fabricius**

– Univoltine (typically May–June). Rare, restricted to mountainous parts of Iberia; known from the Pyrenees, the Sistema Central, Serra do Gerês, Sistema Ibérico, and Sierra de Cazorla[7] .... ***nigrospina*** **Thomson**

40 Depression of T1 sparsely punctate, punctures separated by more than 2 puncture diameters. Nominally univoltine, flying only in the spring[8] .... ***tibialis*** **(Kirby)**

– Depression of T1 densely punctate, punctures separated by 0.5 puncture diameters. Bivoltine, flying in the spring and the summer[8] .... ***bimaculata*** **(Kirby)**

41 (24) Hairs of the tibial scopae clearly plumose, with a majority of strongly branched hairs **42**

– Hairs of tibial scopae entirely simple, or with at most a mixture of simple and scattered and weakly branched hairs..**50**

42 Terga metallic blue, densely punctate, punctures separated by 1 puncture diameter .... ***bellidis*** **Pérez**

– Terga variably coloured, but never metallic blue. Densely punctate or not **43**

43 Terga with discs extensively red-marked (some dark individual of *A. marginata* Fabricius with red markings restricted to the base of the tergal margins) **44**

– Terga dark, at most with depressions lightened, never with red markings at the base of the tergal depressions..**45**

44 Clypeus with fore margin slightly upturned. Foveae short, ventrally reaching only to the level of the antennal insertions. Tibial scopae uniformly yellowish..***pellucens*** **Pérez**

– Clypeus with fore margin straight, not upturned. Foveae long, ventrally extending beyond the level of the antennal insertions. Tibial scopae bicoloured, black-brown dorsally, brownish-white ventrally. Associated with scabious (former Dipsacaceae = Caprifoliaceae) ....***marginata*** **Fabricius**

45 Tibial scopae with short hairs, at most half the length of the diameter of the hind tibia at its maximum apical width............. ***ranunculi*** **Schmiedeknecht**

– Tibial scopae with long hairs, clearly exceeding half the length of the diameter of the hind tibia at its maximal apical width.....................................**46**

46 Fovea narrow, dorsally occupying ⅓ of the space between the compound eye and the lateral ocellus, clearly narrowing ventrally to half its dorsal width.

7 These two taxa cannot be separated morphologically. Association must be made with males, or genetic barcodes generated.

8 These two taxa are challenging to separate in the female sex due to extreme variation in colouration. Further genetic work is needed to clarify species boundaries in Iberia and more broadly. Association should be made with males.

Mid and hind basitarsi and hind tibiae lightened orange-yellow (subgenus *Chrysandrena* Hedicke) **47**

– Fovea broader, dorsally occupying at least ½ the space between the compound eye and the lateral ocellus, not narrowed ventrally. Basitarsi and hind tibiae dark.. **49**

47 Clypeus and scutellum strongly shagreened and matt ....***hesperia* Smith**

– Clypeus and scutellum at least partially shiny **48**

48 Disc of scutum shiny. Scutellum with uniformly light hairs. A2 as long as A3+4. Restricted to temperate areas in northern Portugal and Spain........... ....***fulvago* (Christ)**

– Disc of scutum shagreened and dull. Scutellum with intermixed light and dark brown to black hairs. A2 as long as A3+4+5. Found in Mediterranean areas from southern Portugal to southern and eastern Spain ....***fertoni* Pérez**

49 Process of the labrum large, as long as broad, ventral surface covered with latitudinal wrinkles (Fig. 73D). Foveae dorsally poorly defined, not strongly impressed. Terminal fringe composed of simple dark hairs. Flying in the summer (June-August), associated with Dipsacaceae (=Caprifoliaceae) ....***mucida* Kriechbaumer** (*partim*, 2nd generation)

– Process of the labrum twice as broad as long, without wrinkles. Foveae dorsally strongly impressed and therefore well-defined. Terminal fringe composed of densely plumose orange hairs. Flying in the spring (April-May), Associated with yellow Cichorioideae (Asteraceae)...........***alluaudi* Benoist**

50 (41) Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate (Fig. 65E, c.f. Fig. 79A). Mesepisternum and dorsolateral parts of the propodeum with dense network of raised rugosity................**51**

– Propodeal triangle not strongly defined by lateral carinae with its internal surface rugose-areolate (Fig. 65F–H). Mesepisternum and dorsolateral parts of the propodeum with or without dense network of raised rugosity.. **54**

51 Forewing with two submarginal cells. Clypeus with longitudinal striations. .... ***lagopus* Latreille**

– Forewing with three submarginal cells. Clypeus without longitudinal striations **52**

52 Hind tibiae usually orange. Foveae clearly medially constricted. Terga without hair bands, T2 laterally without a pair of small foveae. Terminal fringe orange..***haemorrhoa* (Fabricius)**

– Hind tibiae always dark. Foveae lacking medial constriction. Terga in fresh specimens with apical white hair bands, T2 laterally with a pair of small foveae. Terminal fringe whitish-yellow **53**

53 Process of the labrum clearly deeply emarginate........***colletiformis* Morawitz**

– Process of the labrum triangular, anterior margin truncate, never emarginate.. ***miegiella* Dours**

54 (50) Scutum and scutellum with short squamous hairs (Figs 33C, D, 43A, 45C, 46B) **55**

– Scutum and scutellum without squamous hairs. If specimen shows longer semi-squamous hairs (e.g. *A. farinosa* Pérez, Fig. 45D), continue here **63**

55 Ocelloccipital distance at least three times the diameter of a lateral ocellus (Figs 33B, 43B). Large bees, exceeding 11 mm in length **56**

– Ocelloccipital distance less than two times the diameter of a lateral ocellus. Smaller bees, exceptionally reaching 11 mm in length.......... **60**

56 Dorsolateral faces of the propodeum clearly, densely, and deeply punctate, punctures separated by <0.5 puncture diameters, with shiny interspaces **57**

– Dorsolateral faces of the propodeum either impunctate, with dense network of raised rugosity, or with shallow and sparser punctures, punctures separated by 0.5–2 puncture diameters, interspaces dull.......... **59**

57 Pubescence of scutum weakly squamous, anterior dorsolateral corners of scutum with pubescence longer, clearly exceeding width of antennae in length. Terga always predominantly red. Terga with clear apical hair bands. Punctation of T1 slightly spaced, punctures separated by 1–2 puncture diameters. Restricted to eastern and south-eastern Spain .... ***nilotica* Warncke**

– Pubescence of scutum short and strongly squamous, anterior dorsolateral corners of scutum with pubescence short, clearly shorter than width of antennae. Terga variable, red to black or any intermediate combination. Terga with or without clear apical hair bands. Punctation of T1 denser, punctures separated at most by 1 puncture diameter.......... **58**

58 A3 exceeding A4+5 in length. Terga always extensively red-marked (central and south-eastern Spain).......... ***parata* Warncke**

– A3 equalling A4+5 in length. Terga variable, from almost entirely black (Fig. 33D) to rarely entirely red-marked .... ***pruinosa* Erichson**

59 Scutal hairs orange-brown (Fig. 43A). Hind tibiae orange (Fig. 43C). Terga with obscure and narrow brownish-yellow hair bands (Fig. 43D). Terminal fringe orange.......... ***limbata dusmeti* Warncke**

– Scutal hairs black and whitish-brown. Hind tibiae dark. Terga with clear and thick white apical hair bands. Terminal fringe dark brown .... ***lateralis* Morawitz**

60 T1 strongly and densely punctate, interspaces shiny (Fig. 46D). Mesepisternum evenly rounded ventrally.......... ***oviventris* Pérez**

– T1 weakly and obscurely punctate, underlying surface shagreened. Mesepisternum ventrally with an indentation anterior to the attachment point of the mid leg.......... **61**

61 Clypeus without latitudinal ridges. T3–4 laterally with clear squamous hairs between the disc and marginal areas. Terga usually extensively red-marked. Basitarsi and hind tibiae orange .... ***hystrix* Schmiedeknecht**

– Clypeus with latitudinal ridges. T3–4 laterally without squamous hairs. Terga never red marked. Legs dark.......... **62**

62 T2–3 laterally strongly shagreened, with obscure and scattered punctures... ....***aeneiventris*** **Morawitz**

– T2–3 laterally finely shagreened, clearly and densely punctate, punctures separated by 0.5 puncture diameters .... ***hedikae*** **Jäger**

63 (54) Viewed laterally, propodeal corbicula with internal surface (lateral faces of the propodeum) glabrous AND propodeal corbiculae complete (possessing both a dorsal and anterior fringe) (Fig. 66A; subgenus *Simandrena*) **64**

– Propodeal corbiculae either incomplete (possessing only a dorsal fringe) AND/OR internal surface with hairs **74**

64 Tibial scopae bicoloured, dorsally dark and ventrally pale **65**

– Tibial scopae unicolourous, dorsally and ventrally light **68**

65 Fovea extremely broad, occupying entirety of space between the compound eye and the lateral ocellus (Fig. 66B). T1 extremely densely punctate, punctures separated by <0.5 puncture diameters, with shiny interspaces. Very rare, known only from one specimen Cádiz .... ***rhypara*** **Pérez**

– Fovea narrower, not occupying entirety of space between the compound eye and the lateral ocellus. T1 strongly shagreened, impunctate or with scattered punctures..**66**

66 T2 impunctate. A2 longer than A3+4, almost as long as A3+4+5............... ....***vetula*** **Lepeletier**

– T2 with fine and dense punctures, punctures separated by 0.5 puncture diameters. A2 as long as A3+4 ....**67**

67 Terga with thick white apical hair bands in fresh specimens (Fig. 27D). Foveae with outer margin straight, not deviating from the inner margins of the compound eyes ....***cilissaeformis*** **Pérez**

– Terga with at most obscure narrow brownish hair bands. Foveae with outer margin constricted, clearly deviating from inner margins of the compound eyes submedially (Fig. 66C) ....***antigana*** **Pérez**

68 Tibial scopae with short hairs, dorsally these hairs not greatly exceeding the width of a lateral ocellus. Metasoma with punctures on tergal discs dense medially, becoming sparse laterally...**69**

– Tibial scopae with long hairs, very clearly greatly exceeding the width of a lateral ocellus. Metasoma with consistently dense punctures, not becoming sparser laterally **70**

69 Scutum medially strongly shagreened and dull (Fig. 66D). In fresh specimens, tergal hair bands short, not noticeably surpassing the apex of the tergal margins. Hind tibiae and basitarsi usually orange, but can be entirely dark. Restricted to temperate areas in northern Spain ....***dorsata*** **(Kirby)**

– Scutum medially polished and shiny (Fig. 66E) or extensively but weakly shagreened with a silky shine. In fresh specimens, tergal hair bands long, clearly surpassing the apex of the tergal margins. Hind tibiae and basitarsi usually dark, occasionally lightened orange-brown. Common throughout Iberia ....***propinqua*** **Schenck**

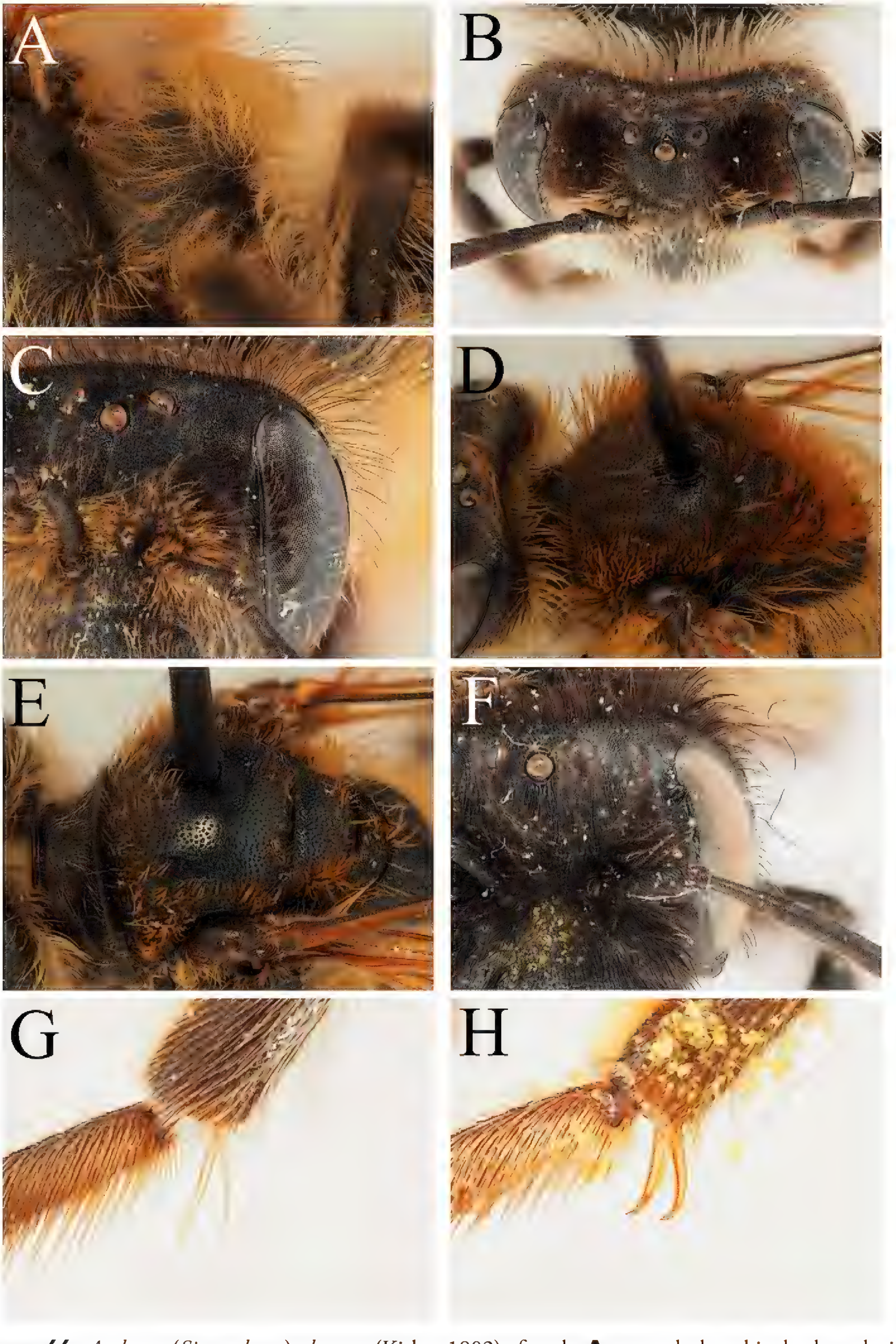

Figure 66. *Andrena* (*Simandrena*) *dorsata* (Kirby, 1802), female **A** propodeal corbicula, lateral view **D** scutum, dorsolateral view; *Andrena* (*Simandrena*) *rhypara* Pérez, 1903, female **B** foveae, dorsal view; *Andrena* (*Simandrena*) *antigana* Pérez, 1895, female **C** fovea, dorsofrontal view; *Andrena* (*Simandrena*) *propinqua* Schenck, 1853, female **E** scutum, dorsolateral view; *Andrena* (*Melandrena*) *bicolorata* (Rossi, 1790), female **F** fovea, dorsofrontal view; *Andrena* (*Notandrena*) *nigroviridula* Dours, 1873, female **G** hind tibial spurs, dorsal view; *Andrena* (*Notandrena*) *varuga* Warncke, 1975, female **H** hind tibial spurs, dorsal view.

70 Disc of T1 strongly and densely punctate, punctures separated by <1 puncture diameter **71**

– Disc of T1 finely and sparsely punctate, punctures separated by >1 puncture diameter **72**

71 Clypeus with pattern of raised latitudinal ridges .... ***combinata* (Christ)**

– Clypeus smooth in the middle, at most transversely wrinkled at the base, ventro-laterally with slight longitudinal wrinkles .... ***lepida* Schenck**

72 Head and mesosoma white-haired. Clypeus smooth and shiny between punctures. Restricted to areas close to the Pyrenees .... ***thomsonii* Ducke**

– Head and mesosoma with rich chestnut-brown hair. Clypeus shagreened and dull between punctures **73**

73 T2–4 with discs finely and densely punctate. Terminal fringe dark brown. Hind tibiae sometimes lightened orange. More widespread across Iberia[9] .... ***congruens* Schmiedeknecht**

– T2–4 with discs sparsely and obscurely punctate. Terminal fringe reddish-brown. Restricted to the Pyrenees and Cantabrian Mountains[9] .... ***confinis* Stöckhert**

74 (63) Fovea strongly constricted medially, strongly diverging from the inner margin of the compound eye dorsally (Fig. 66F; former subgenus *Hyperandrena* Pittioni) **75**

– Fovea not constricted medially, not strongly diverging from the inner margin of the compound eye **76**

75 Tibial scopae unicolourous black. Mesosoma entirely covered with light grey hairs .... ***bicolorata* (Rossi)**

– Tibial scopae dorsally black, ventrally orange-red. Mesosoma entirely covered with dark to light brown hairs .... ***florentina* Magretti**

76 (74) At least some tergal discs extensively red-marked (Fig. 41D) **77**

– Tergal discs never red-marked, at most with tergal margins lightened **83**

77 Small bees, never exceeding 9 mm in length. Fovea narrow, at most occupying ⅓ of space between the compound eye and the lateral ocellus **78**

– Large bees, greater than 11 mm in length. Fovea broader, occupying at least ½ the space between the compound eye and the lateral ocellus **80**

78 Propodeal triangle broad, laterally delineated with raised straight carinae, internal surface with fine network of raised rugae. Head and scutum without metallic reflections .... ***labiata* Fabricius**

– Propodeum narrow, poorly defined, lacking lateral carinae, internal surface at most with short and weak rugae basally, surface with fine granular shagreenation. Head and scutum with strong or weak metallic reflections **79**

9 These two species are challenging to separate, and there may be taxonomic complexity in Iberia. Further study is required.

79 Clypeus medially smooth and shiny between the punctures. Scutum anteriorly shagreened, medially becoming smooth and shiny, irregularly but clearly punctate, with strong greenish metallic reflections .... ***binominata* Smith**

– Clypeus medially completely shagreened and dull. Scutum shagreened and shallowly punctate, with weak bronzy metallic reflections .... ***leucophaea* Lepeletier**

80 Tibial scopae unicolourous light orange. Propodeal triangle clearly delineated laterally by fine carinae, internal surface with fine network of raised rugae. Clypeus densely and uniformly punctate, without a longitudinal impunctate midline.. ***schencki* Morawitz**

– Tibial scopae bicoloured, dorsally dark, ventrally light (Fig. 41A). Propodeal triangle poorly defined, lacking lateral carinae, internal surface more or less smooth, without network of rugae (Fig. 41C). Clypeus densely or sparsely punctate, with clear longitudinal impunctate midline **81**

81 Terga strongly and densely punctate, punctures separated by 1 puncture diameter. Compound eyes with inner margins diverging ventrally (Fig. 41B). Excluding impunctate midline, clypeus comparatively sparsely punctate, punctures separated by 1–2 puncture diameters .... ***florea* Fabricius**

– Terga shallowly and obscurely punctate, punctures separated by 2–3 puncture diameters. Compound eyes with internal margins more or less parallel. Excluding impunctate midline, clypeus comparatively densely punctate, punctures separated by 0.5–1 puncture diameters..................................**82**

82 T1–2 with long hair, equalling the length of the hair on the mesosoma[10] ... . ***trimmerana* (Kirby)** (*partim*, light form)

– T1–2 with shorter hair, never equalling the length of the mesosomal hair[10] .... ***rosae* Panzer** (*partim*, light form)

83 (76) Head, mesosoma, or tergal discs with metallic reflections (note, *A. nigroaenea* (Kirby) can have bronzy reflections on the terga; if the tibial scopae is composed of orange-red hairs or the tibial scopae is mainly dark with only the ventral hairs orange, go to 206) **84**

– Body without metallic reflections...**91**

84 Mesosoma with strongly contrasting pattern of black and white hairs; mesosoma anteriorly and posteriorly with white hairs, medially with a band of black hairs...**85**

– Mesosoma without strongly contrasting pattern of black and white hairs......**86**

85 Wings infuscate over their apical 2/3rds. Sterna laterally and apically with black hairs. A3 comparatively shorter, shorter than A4+5. Bivoltine (April–

10 Beware of abraded specimens when dealing with these two species.

May; July–August), restricted to mountains in northern Spain and the Pyrenees[11] ....***barbareae* Panzer**

– Wings hyaline over the majority of their area, only slightly darkened apically. Sterna laterally and apically with white hairs. A3 comparatively longer, equalling A4+5. Univoltine (April–May), more widespread across northern Portugal and Spain[11] .... ***cineraria* (Linnaeus)**

86 Scutum uniformly densely shagreened and completely dull over its entire surface, extremely densely punctate, punctures shallow, flat, and confluent. Mesosoma and discs of T1–2 dorsally with long chestnut-brown hair......... .... ***doursana* Dufour**

– Scutum either at least partly shiny or less densely punctate, punctures clearly separated by at least 1 puncture diameter. Mesosoma and discs of T1–2 never with long chestnut-brown hair, either glabrous, with shorter hairs, or with hairs of a different colour **87**

87 Terga clearly punctate, punctures separated by up to 2 puncture diameters. **88**

– Terga obscurely and sparsely punctate, punctures separated by 4–5 puncture diameters **89**

88 Fovea broad, occupying 2/3rds of the space between the compound eye and a lateral ocellus. Tergal punctation comparatively sparse, punctures separated by 1–2 puncture diameters. Scutum medially becoming smooth and shiny between the punctures. Restricted to south-western Spain (Huelva, Sevilla) .... ***laurivora* Warncke**

– Fovea narrow, occupying less than ½ the space between the compound eye and a lateral ocellus. Tergal punctation dense, punctures separated by up to 1 puncture diameter. Scutum uniformly shagreened and dull. Restricted to the Pyrenees... ***viridescens* Viereck**

89 Larger species, 11–12 mm. Clypeus shagreened and dull over the majority of its surface. Fovea narrow, but uniformly wide along their length, not narrowing ventrally ....***aerinifrons* Dours**

– Smaller species, under 9 mm. Clypeus shiny over the majority of its area. Foveae narrow, but also narrowing ventrally to approximately half of their dorsal width...**90**

90 Scutum with clear metallic green reflections. Hind tibial spurs straight (Fig. 66G)...***nigroviridula* Dours**

– Scutum dark, with at most weak and obscure metallic reflections. Hind tibial spurs strongly bent at their apexes (Fig. 66H) .... ***varuga* Warncke**

91 (83) Small black species without a keel laterally on the pronotum, body length under 8 mm, or if up to 10 mm then with lateral faces of the propodeum

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11 These two species are challenging to separate morphologically.

with clear pattern of raised star-shaped wrinkles (all members of the subgenera *Aciandrena*, *Graecandrena*, *Micrandrena*)[12] **92**
– Species larger than 9 mm in length or with pronounced keel on the pronotum laterally **138**
92 Propodeal triangle smooth, not defined laterally by raised carinae, with internal surface lacking network of raised rugosity, at most with very short rugae at the base of the propodeal triangle (Fig. 67A) **93**
– Propodeal triangle either strongly defined by raised carinae, or with internal surface with network of raised rugosity covering at least the basal half (Fig. 67B; note, take care with *A. tenuistriata*, for which the lateral parts of the propodeal triangle present granular shagreen, Fig. 67C) **106**
93 Clypeus with clear raised longitudinal striations (Fig. 67D) **94**
– Clypeus without any striations **96**
94 Clypeus flattened, medially slightly depressed, weakly concave. Process of the labrum short, twice as broad as long, forming a triangular point. A3 almost as long as A4+5+6. Central and eastern Spain only .... ***fria* Warncke**
– Clypeus evenly arched. Process of the labrum narrower, as long as broad. A3 only slightly exceeding A4+5. More widespread **95**
95 Tibial scopa composed of unicolourous light hairs. T3 impunctate, with weak apical yellowish hair band, marginal area at most weakly depressed. Widespread across Iberia .... ***longibarbis* Pérez**
– Tibial scopa pale ventrally, dark dorsally. T3 with obscure punctures, with strong apical white hair band overlying the clearly depressed marginal area. Restricted to sandy and usually coastal habitats in southern Iberia .... ***orana* Warncke**
96 Foveae not ventrally narrowed, in their lower half at least half as wide as the distance from the inner margin of the compound eye (Fig. 67E) **97**
– Foveae ventrally narrowed, in their lower half as wide as the distance from the inner margin of the compound eye (Fig. 67F, G) **98**
97 T2–4 with narrow, widely interrupted hair bands. Wing venation brownish. Clypeus shagreened to smooth and shiny, densely punctate, punctures separated by 1 puncture diameter. Process of the labrum narrow and triangular with a pointed tip (Fig. 67E). Larger, 8 mm. Widespread across Iberia .... ***pandosa trigona* Warncke**
– T2–4 with complex wide and dense white hair bands. Wing venation light yellow. Clypeus uniformly shagreened, irregularly punctate, punctures separated by 1–3 puncture diameters. Process of the labrum with the apical margin truncate. Smaller, 6 mm. Rare, known only from central Spain .... ***montarca* Warncke**

12 Note, this couplet is not intended to include small examples of members of the subgenera *Leucandrena* Hedicke, 1933 and *Notandrena*. Therefore, small individuals with a clearly keeled pronotum should follow the alternative couplet.

98 Tergal discs clearly and regularly punctate, punctures separated by 1 puncture diameter, with punctures extending onto marginal areas...................... ....*fulica* **Warncke**

– Terga either impunctate or obscurely punctate, but punctures never extending onto marginal areas..**99**

99 Supraclypeal area covered with longitudinal striations (Fig. 67F) **100**

– Supraclypeal area without any striations (Fig. 67G) **105**

100 Longitudinal striations on the paraocular areas strong and pronounced, continuing ventrally to the lateral margins of the clypeus without becoming weaker. Clypeus flattened, with distinct longitudinal impression or furrow medially. Restricted to the extreme north-east of Spain...................... ***impunctata*** **Pérez**

– Longitudinal striations on the paraocular areas ventrally extending to the lateral margins of the clypeus but here clearly weaker than their strength adjacent to the foveae. Clypeus either domed or if flattened then without longitudinal impression **101**

101 Clypeus strongly flattened, coarsely shagreened and dull over almost its entirely surface, apical margin narrowly and obscurely shiny; clypeus with shallow and obscure punctures that disappear into the underlying shagreen, punctures separated by 1–2 puncture diameters (Fig. 67F)............ .... ***verticalis*** **Pérez**

– Clypeus either domed, or if flattened then with a broad shiny apical margin (at least as broad at the width of a flagellum) and punctures that are clearly visible against the underlying shagreenation..**102**

102 A3 exceeding the length of A4+5. Striations of supraclypeal area weakly continue onto clypeus basally and laterally, here shagreened with weakly raised striations. Clypeus shagreened basally and laterally, becoming smooth and shiny medially and apically, with narrow medial shagreened projection, shagreenation thus forming a weak trident shape. Known only from a few specimens from the extreme south of Spain, probably representing an undescribed species (Málaga, Sevilla) ....**aff *mica* Warncke**

– A3 at most equalling A4+5. Striations of supraclypeal area not continuing onto clypeus, entire clypeus free of even a hint of striations **103**

103 Clypeus with fine punctures, punctures separated by 1–3 puncture diameters. Underlying shagreenation weak basally. Process of the labrum slightly broader than long. Presence and distribution in Iberia unclear ....***abjecta*** **Pérez**

– Clypeus with strong and coarse punctures, punctures separated by 0.5–2 puncture diameters. Underlying shagreenation strong and coarse basally. Process of the labrum narrow, slightly longer than broad **104**

104 Scutellum polished and shiny between punctures. Clypeus domed and somewhat flattened medially. Restricted to south-eastern Spain (Alicante, Almería, Granada, Murcia) ....***tenostra*** **Warncke**

– Scutellum dull and shagreened. Clypeus largely flattened across its entire surface. More widespread across Iberia.................................***alma*** **Warncke**

105 Larger, 7–8 mm. T3–4 with discs obscurely punctate. Hind basitarsi lightened orange. Nervulus of the forewing interstitial to weakly antefurcal. Shagreenation of the clypeus becoming weaker at its apical margin .... ***nebularia*** **Warncke**

– Smaller, 4–5 mm. T3–4 with discs impunctate. Hind basitarsi dark. Nervulus of the forewing strongly antefurcal. Clypeus uniformly shagreened .... ***vacella*** **Warncke**

106 Lateral shoulders of T1 with a pair of strongly produced sharp ridges (Fig. 67H). Terga shiny with mixture of small and large punctures. Mesepisternum depressed above the insertion point of the mid legs. Rare, restricted to central Spain .... ***taxana*** **Warncke**

– Lateral shoulders of T1 never with clearly produced ridges, or if with ridges (*A. strohmella* Stöckhert) then terga never shiny and deeply punctate. Tergal punctation otherwise. Mesepisternum evenly rounded **107**

107 Hind tibiae and basitarsi orange, tibial scopa composed of extremely short hairs. Restricted to the Pyrenees and the Cantabrian Mountains, flying July–August, associated with *Potentilla* (Rosaceae) .... ***tarsata*** **Nylander**

– Hind legs dark, tibial scopa with hairs normal, not extremely short **108**

108 Foveae long, dorsally extent reaching a line parallel to the hind margin of the lateral ocelli, foveae deeply impressed. Propodeal triangle not laterally delineated by carinae, internal surface weakly elevated, with irregular raised rugae that do not cover the entire area. Terga laterally with loose, white interrupted hair bands. Restricted to cooler areas in and around the Pyrenees and Cantabrian Mountains, flying July–August .... ***coitana*** **(Kirby)**

– Foveae shorter, not reaching level of the lateral ocelli dorsally, only weakly impressed. Propodeal triangle clearly delineated laterally by carinae, internal surface evenly and regularly covered by fine network of raised rugae. Terga with lateral hair bands or not **109**

109 Foveae either uniformly narrow or strongly narrowed ventrally, in their ventral half at most as wide as the distance to the inner margin of the compound eye **110**

– Foveae not or only weakly narrowed ventrally, in their ventral half clearly wider than the distance to the inner margin of the compound eye **115**

110 Clypeus with longitudinal striations (c.f. Fig. 67D) **111**

– Clypeus without striations **112**

111 Disc of T1 shagreened and dull. T2–4 with hair bands long, longer than the diameter of a flagellum. Scutum uniformly shagreened and dull. Restricted to the extreme north-east of Spain .... ***distinguenda*** **Schenck**

– Disc of T1 polished and shiny, contrasting the shagreened marginal area. T2–4 with short hair bands, shorter than the diameter of a flagellum. Scutum laterally shagreened, medially smooth and shiny. Widespread throughout Iberia .... ***nitidula*** **Pérez**

112 T1 finely shagreened to polished and shiny. Mesonotum densely and strongly punctate **113**

– T1 strongly shagreened and dull. Mesonotum finely and sparsely punctate. **114**

113 Foveae uniformly narrow, dorsally narrower than the diameter of a flagellum. Disc of T1 with scattered punctures, separated by at least 2 puncture diameters .... ***fabrella* Pérez**

– Foveae dorsally broader than ventrally, dorsally as wide as the diameter of a flagellum. Disc of T1 more densely punctate, punctures separated by 0.5–1 puncture diameters .... ***nana* (Kirby)**

114 Foveae uniformly narrow, dorsally narrower than the diameter of a flagellum. Terga impunctate. Clypeus evenly domed, densely shagreened and dull. Associated with Cistaceae .... ***djelfensis* Pérez**

– Foveae dorsally broader than ventrally, dorsally as wide as the diameter of a flagellum. Terga obscurely punctate. Clypeus weakly three-faced, anterior margin shiny. Associated with Brassicaceae .... ***tenuistriata* Pérez**

115 Large species, 10 mm in length. Clypeus densely covered with latitudinal wrinkles. Lateral faces of the propodeum covered with pattern of raised star-shaped wrinkles .... ***ampla* Warncke**

– Most species smaller. Clypeus without latitudinal wrinkles and propodeum without pattern of raised star-shaped wrinkles **116**

116 Larger species, 8–9 mm. Discs of T1–3 extremely densely punctate, punctures almost confluent, separated by <0.5 puncture diameters. Clypeus densely punctate, punctures separated by 1 puncture diameter, interspaces with weakly raised ridges that form subtle pattern of longitudinal striations. Rare, known from eastern Spain (Jáen, Soria, Teruel) .... ***vaulogeri* Pérez**

– Smaller, usually shorter than 8 mm. Discs of T1–3 less densely punctate, punctures separated by >1 puncture diameter, or if punctures dense, then much smaller than 8 mm in length. Clypeus without pattern of longitudinal ridges or striations **117**

117 T3–4 with the marginal areas strongly depressed relative to the discs (Fig. 68A–E) 118

– T3–4 with the marginal areas only superficially depressed (Fig. 68F, G)...... .... **131**

118 T2–3 laterally without a gradulus **119**

– T2–3 laterally with gradulus present (c.f. Fig. 68F, G) **122**

119 Tergal discs and marginal areas completely smooth and shiny, without any shagreenation (Fig. 68B). Found in the Sistema Central to west and north-western Iberia. Associated with *Sedum* (Crassulaceae) .... ***omnilaevis* Wood**

– At least tergal discs shagreened **120**

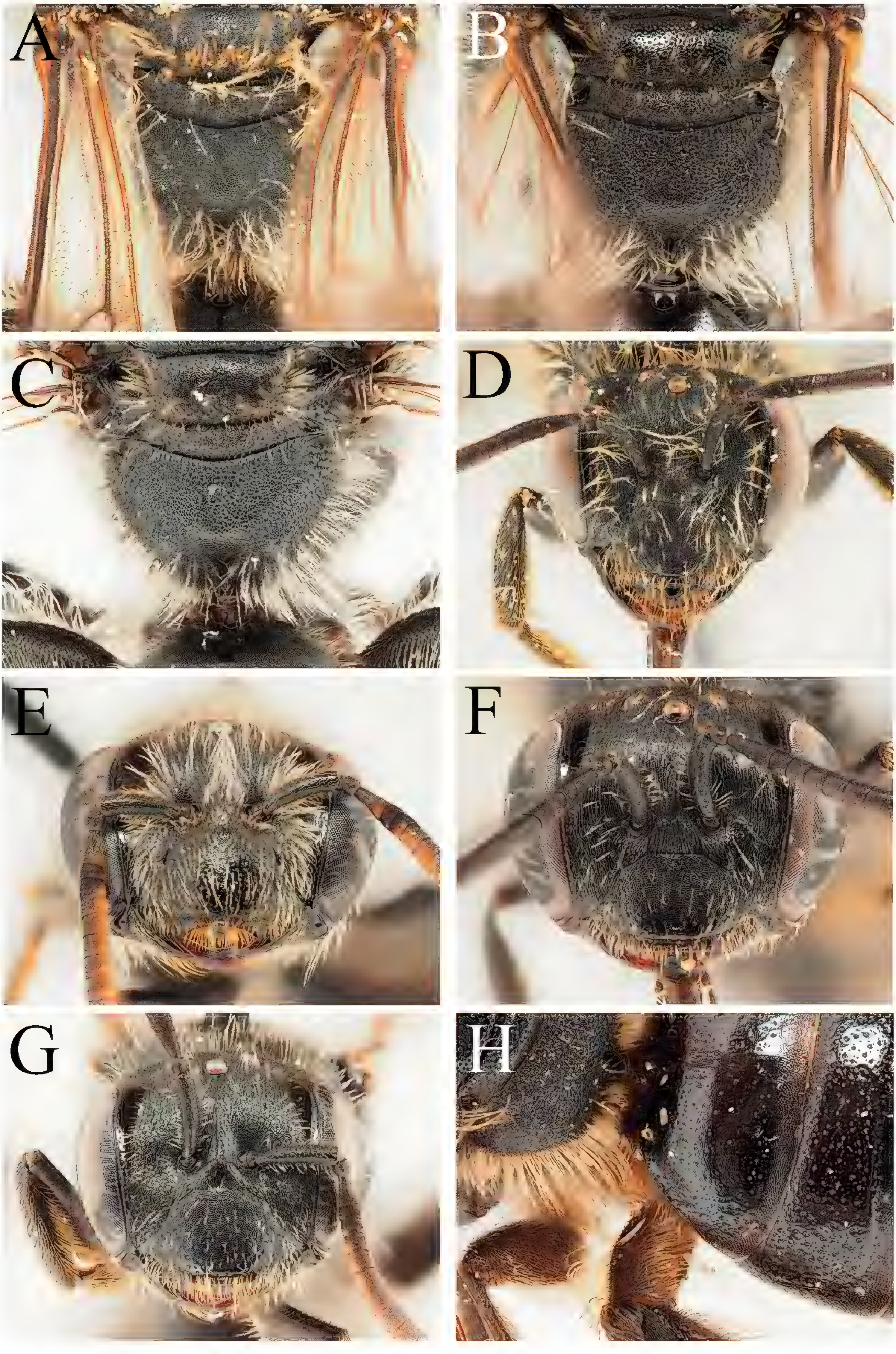

Figure 67. *Andrena* (*Micrandrena*) *longibarbis* Pérez, 1895, female **A** propodeum, dorsal view **D** clypeus, frontal view; *Andrena* (*Micrandrena*) *spreta* Pérez, 1895, female **B** propodeum, dorsal view; *Andrena* (*Micrandrena*) *tenuistriata* Pérez, 1895, female **C** propodeum, dorsal view; *Andrena* (*Micrandrena*) *pandosa trigona* Warncke, 1975, female **E** face, frontal view; *Andrena* (*Graecandrena*) *verticalis* Pérez, 1895, female **F** face, frontal view; *Andrena* (*Graecandrena*) *nebularia* Warncke, 1975, female **G** face, frontal view; *Andrena* (*Parandrenella*) *taxana* Warncke, 1975, female **H** T1, dorsal view.

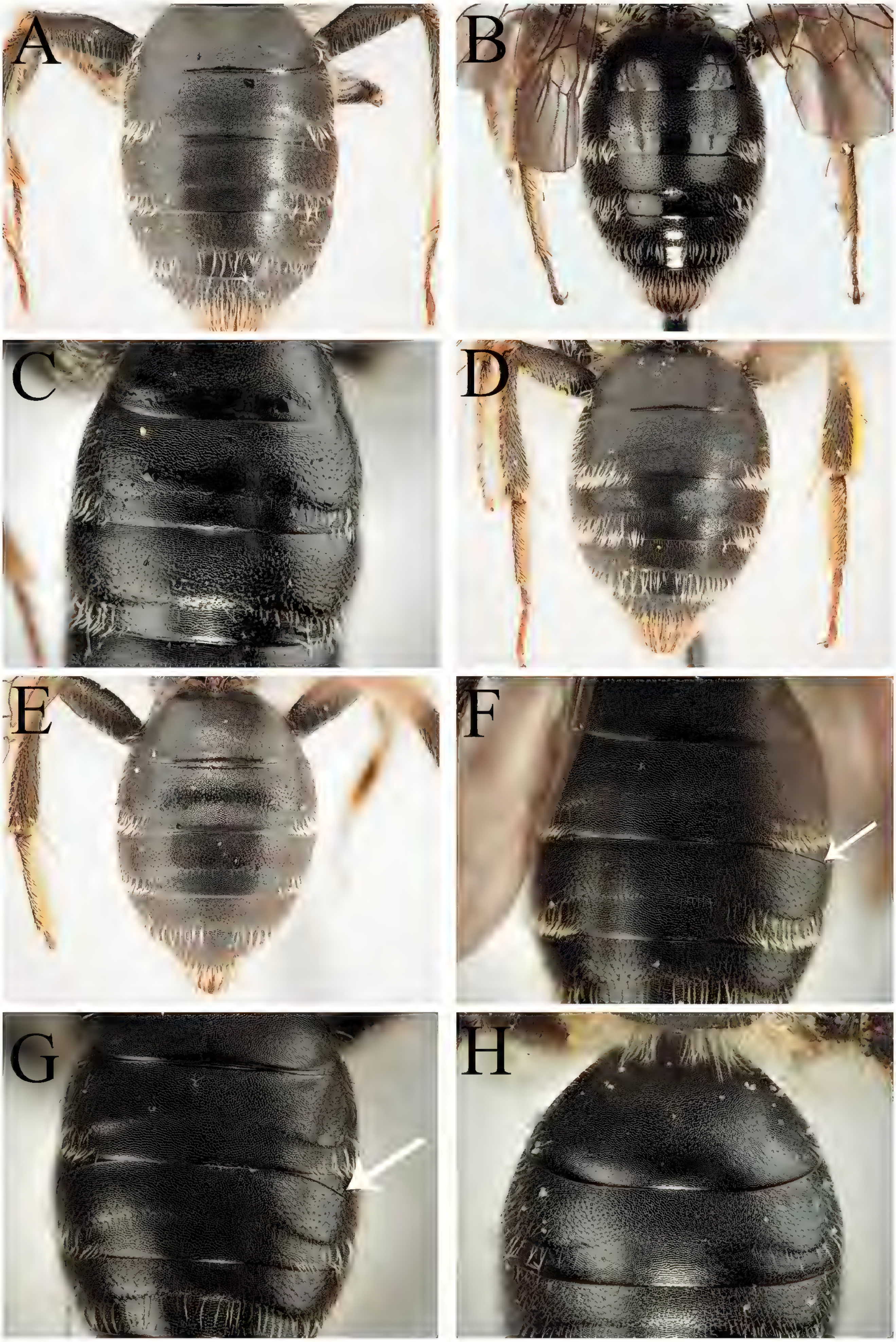

Figure 68. *Andrena* (*Micrandrena*) *spreta* Pérez, 1895, female **A** terga, dorsal view; *Andrena* (*Micrandrena*) *omnilaevis* Wood, 2020, female **B** terga, dorsal view; *Andrena* (*Micrandrena*) *anthrisci* Blüthgen, 1925, female **C** terga, dorsal view; *Andrena* (*Micrandrena*) *pauxilla* Stöckhert, 1935, female **D** terga, dorsal view; *Andrena* (*Micrandrena*) *bayona* Warncke 1975, female **E** terga, dorsal view; *Andrena* (*Micrandrena*) *minutula* (Kirby, 1802), female **F** terga, dorsal view (gradulus indicated by white arrow); *Andrena* (*Micrandrena*) *minutuloides* Perkins, 1914, female **G** terga, dorsal view (gradulus indicated by white arrow); *Andrena* (*Micrandrena*) *falsifica* Perkins, 1915, female **H** terga, dorsal view.

120 Terga with marginal areas not noticeably differentiated structurally from discs, strongly and densely shagreened and dull (Fig. 68D). Tergal discs essentially impunctate, with any obscure punctures disappearing into dense shagreenation. Scutum densely punctate, punctures separated by 0.5–1 puncture diameter .... ***pauxilla*** **Stöckhert**

– Terga with marginal areas noticeably shinier than discs, with weaker shagreenation. Tergal discs with clear punctures visible against the underlying shagreenation (Fig. 68C). Scutum less densely punctate, punctures separated by 1–2 puncture diameters.. **121**

121 Depressed tergal margins polished and shiny, clearly shinier than shagreened tergal discs. In dorsal view, lateral hairs at the base of the marginal area of T2 longer, erect, projecting at a 45° angle, breaking profile of metasoma laterally. Margin of T2 comparatively strongly depressed. Restricted to the Pyrenees and the Cantabrian Mountains .... ***semilaevis*** **Pérez**

– Depressed tergal margins shagreened, similar to and not strongly contrasting shagreened tergal discs (Fig. 68D). In dorsal view, lateral hairs at the base of the margin area of T2 shorter, flat, not projecting, almost parallel with lateral profile of metasoma. Margin of T2 comparatively weakly depressed. Slightly more widespread across central and northern Spain in mountainous areas.. ***anthrisci*** **Blüthgen**

122 Disc of T1 smooth and shiny, clearly punctate, punctures medially separated by 0.5–1 puncture diameter, not extending onto the broad impunctate marginal area. Rare, restricted to the Pyrenees and northern Spain .... ***floricola*** **Eversmann**

– Disc of T1 never smooth and shiny, always at least partially shagreened, punctate or not **123**

123 Gena entirely smooth and shiny, without any shagreenation. Scutum and scutellum polished and shiny. T2–3 with discs strongly and densely punctate, punctures separated by 1 puncture diameter (Fig. 68E). Restricted to dry and steppic habitats in central Iberia including northern Portugal .... ***bayona*** **Warncke**

– Gena shagreened and dull, at most with a narrow shiny strip along the outer margin of the compound eye. Scutum and scutellum variable, usually at least partially shagreened. T2–3 usually less densely and strongly punctate **124**

124 Head comparatively long, only slightly shorter than broad (Fig. 48B). Discs of T1–3 extremely densely punctate, punctures separated by 0.5–1 puncture diameters (Fig. 48D). Restricted to high-altitude on the Sierra Nevada .... ***ortizi*** **sp. nov.**

– Head shorter, clearly broader than long. T1–3 never so densely punctate, punctures when visible separated by at least 1 puncture diameter.......... **125**

125 Propodeal triangle poorly defined (Fig. 20E, F), lateral carinae disappearing medially, not extending from the base (metanotum) to the apex (vertical face of the propodeum). Tergal discs weakly to strongly shiny............... **126**

– Propodeal triangle well-defined, lateral carinae consistently strong from the base to the apex. Tergal discs weakly to strongly shagreened, never shiny............ **127**

126 Tergal discs entirely shiny, polished, and smooth (Fig. 20H). Scutum and scutellum extensively shiny, without shagreenation .... ***lecana* Warncke**

– Tergal discs at least partially shagreened, never entirely shiny (Fig. 20G). Scutum and scutellum with subtle shagreenation, not smooth and shiny.... .... ***niveata* Friese**

127 T1 laterally with slightly raised corners, visibly projecting and disrupting rounded profile when viewed dorsally. Clypeus slightly flattened centrally, with clear impunctate mid-line between large and well defined clypeal punctures. Terga 2–3 centrally impunctate, laterally with large punctures with raised margins (crater punctures). Restricted to areas close to the Pyrenees .... ***strohmella* Stöckhert**

– T1 laterally without such raised projections, in dorsal view evenly rounded. Clypeus with or without a clear impunctate mid-line. Terga punctation with or without lateral crater punctures. Distribution otherwise **128**

128 Clypeus weakly domed, sparsely punctate, punctures large, separated by 2–3 puncture diameters. T2–3 laterally with large hair-bearing punctures that contrast the underlying shagreenation and do not disappear into it .... ***icterina* Warncke**

– Clypeus more densely punctate, punctures separated by 1–2 puncture diameters. T2–3 laterally with at most obscure punctures............................. **129**

129 Terga comparatively weakly shagreened and finely punctate, punctures relatively clearly visible against background shagreen, punctures extending onto tergal margins, most clearly visible on T1–3. Anterior ½ to ⅓ of clypeus usually polished and shiny. Probably univoltine (March-May). Central, eastern, and southern Spain, rare[13] .... ***exigua* Erichson**

– Terga comparatively strongly shagreened, obscurely punctate, punctures disappearing into underlying shagreenation (Fig. 68A). Tergal margins impunctate. Clypeus usually shagreened, without polished fore-margin[13] **130**

130 Scutum strongly and clearly punctate, punctures separated by 1–2 puncture diameters, underlying surface variable but always at least partially shiny. Bivoltine (March-July). Throughout Iberia, common[13] .... ***spreta* Pérez**

– Scutum obscurely punctate, punctures disappearing into the abundant underlying shagreen, scutum dull. Univoltine (April-May). Iberian distribution

13 These three species are challenging to separate without confidently identified reference material. Most specimens will be *A. spreta* Pérez which is by far the most commonly collected of the three.

unclear, but probably restricted to southern Spain (Cádiz, Málaga)[13] ....***tiaretta* Warncke**

131 Disc of T1 clearly punctate, though sometimes finely and sometimes only punctate basally (Fig. 68H). Disc of T2 more strongly, clearly, and extensively punctate **132**

– Disc of T1 finely to strongly shagreened, at most obscurely punctate with punctures disappearing into the underlying surface sculpture (Fig. 67F, G). Disc of T2 with at most a few punctures laterally..................................**134**

132 Marginal area of T1 wide, strongly thickened, impunctate (Fig. 68H). Restricted to mountainous areas in northern Spain, associated with *Potentilla* (Rosaceae) ....***falsifica* Perkins**

– Marginal area of T1 normal, not widened or thickened **133**

133 Disc of T1 strongly shagreened, predominantly punctured medially. Antennae ventrally at most lightened dark brown. Throughout Iberia, bivoltine..***alfkenella* Perkins**

– Disc of T1 finely shagreened, evenly and finely punctate over its entire area, with shiny interspaces. Antennae ventrally orange. Rare, restricted to northern Spain, univoltine (August–September)...................... ***nanula* Nylander**

134 Process of the labrum narrow, as long as broad. Scutum strongly shagreened and matt, densely punctate, punctures difficult to discern against the strong underlying sculpture. Clypeus sparsely punctate, with obscure and weak latitudinal striations....................................... ***simontornyella* Noskiewicz**

– Process of the labrum wider, broader than long. Scutum less strongly shagreened, with punctures of variable density that are clearly visible against the underlying sculpture. Clypeus variably punctate, but never with latitudinal striations..**135**

135 Clypeus strongly flattened and sparsely punctate, punctures separated on average by more than 2 puncture diameters. Process of the labrum medially emarginate. Associated with *Ornithogalum* (Asparagaceae)......................... .... ***saxonica* Stöckhert**

– Clypeus domed, never strongly flattened, punctures dense or sparse. Process of the labrum truncate or apically rounded.. **136**

136 Clypeus sparsely and obscurely punctate, punctures separated by 2–3 puncture diameters or more. Scutum very sparsely and finely punctate, punctures small, separated by 2–3 puncture diameters, underlying surface shagreened and dull. Restricted to temperate areas close to the Pyrenees .... ***subopaca* Nylander**

– Clypeus clearly punctate, punctures separated by 1–2 puncture diameters. Scutum more densely punctate, punctures larger, separated by up to 2 puncture diameters, underlying surface dull to shiny. Throughout Iberia..................**137**

137 Scutellum shagreened, at most weakly shiny. Scutum more densely punctate, punctures separated by 1 puncture diameter, underlying surface shagreened and dull (1st generation) to weakly shiny (2nd generation). Terga with dense and narrow apical hair bands laterally, individual hairs touching

each other in fresh specimens (Fig. 68F). Foveae not noticeably narrowed ventrally..***minutula* (Kirby)**

– Scutellum always polished and shiny. Scutum less densely punctate, punctures less regular, separated by 1–2 puncture diameters, underlying surface finely shagreened and weakly shiny (1st generation) to smooth and shiny (2nd generation). Terga with sparse apical hair bands, occasionally with some individual hairs touching each other (Fig. 68G; 1st generation), usually with all hairs individually separated (2nd generation). Foveae slightly but distinctively narrowed ventrally.. ***minutuloides* Perkins**

138(91) Clypeus flattened over majority of its surface. Species strongly associated with Fabaceae (subgenus *Taeniandrena*)[14]..**139**

– Clypeus not noticeably flattened. Species not usually associated with Fabaceae **151**

138 Face and foveae black haired. Terminal fringe dark brown (Fig. 69A). Terga with weak and obscure punctures. Known only from central Portugal (Castelo Branco) and south-western Spain (Huelva, Cádiz). Univoltine (March–April) .... ***lusitania* Wood & Ortiz-Sánchez**

– Combination of characters otherwise; either face with pale hairs, terminal fringe light, or tergal densely punctate **140**

140 Terminal fringe composed of dark brown to brownish grey hairs. Hairs flanking the basitibial plate of the hind tibia also dark (Fig. 69B) **141**

– Terminal fringe and hairs flanking basitibial plate of hind tibia light, golden to yellow-orange (Fig. 69C–F) **143**

141 Discs of T2–4 strongly and densely punctate, punctures clearly visible against the underling shagreenation. Widespread throughout Iberia, most common in areas with an Atlantic climate and abundant Genisteae. Bivoltine (typically March–May; June–July) ....***ovatula* (Kirby)**

– Discs of T2–4 obscurely and shallowly punctate, punctures disappearing into background shagreenation. Iberian distribution more restricted (see below) **142**

142 Scutum with punctures shallow and obscure, separated by >1 puncture diameter. T3 with apical hair band interrupted medially. Currently known only from the steppe of central Spain (Guadalajara, Salamanca, Segovia). Univoltine (May–June).. ***ovata* Schenck**

– Scutum with punctures dense and clear, separated by <1 puncture diameter. T3 with apical hair band complete in fresh specimens. Currently only confirmed from the coast of southern Spain (Málaga). Bivoltine (probably February–April; May–June) ....***poupillieri* Dours**

14 Females of this subgenus are highly challenging and in some cases impossible to identify. There are several outstanding taxonomic issues in this subgenus that require in-depth genetic study to resolve, and additional probably undescribed cryptic species are present. Do not expect to identify this group without consulting confidently determined reference material, and ideally barcoded specimens. Minimal characters are given here because of the ongoing lack of taxonomic clarity in this subgenus. See also the key of Praz et al. (2022).

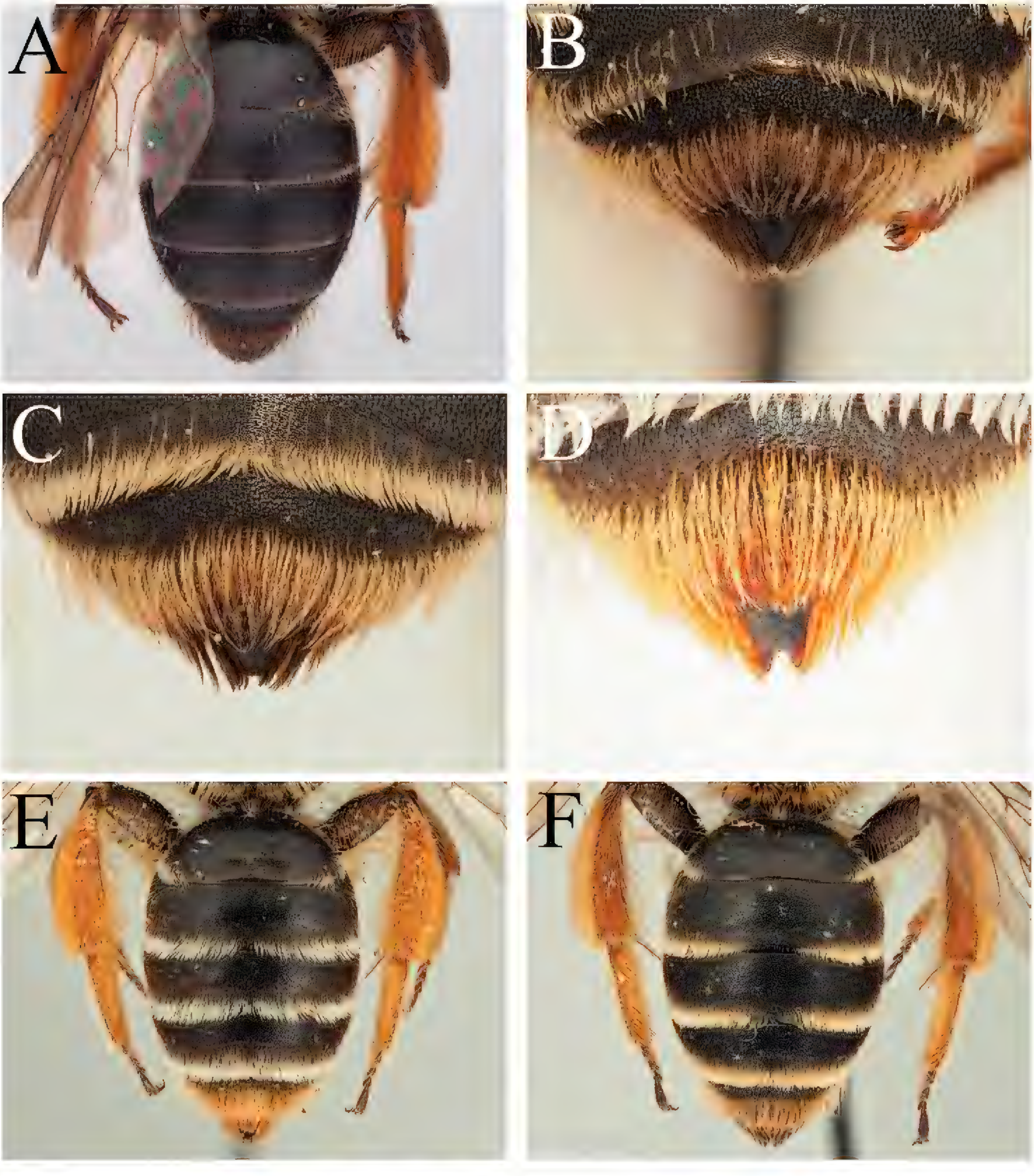

Figure 69. *Andrena* (*Taeniandrena*) *lusitania* Wood & Ortiz-Sánchez, 2022, female **A** terga, dorsal view; *Andrena* (*Taeniandrena*) *ovatula* (Kirby, 1802), female **B** terminal fringe; *Andrena* (*Taeniandrena*) *afzeliella* (Kirby, 1802), female **C** terminal fringe; *Andrena* (*Taeniandrena*) *lathyri* Alfken, 1900, female **D** pygidial plate, posterior view; *Andrena* (*Taeniandrena*) *gredana* Warncke, 1975, female **E** terga, dorsal view; *Andrena* (*Taeniandrena*) *benoisti* Wood & Praz, 2021, female **F** terga, dorsal view.

143 Pygidial plate apically with deep emargination medially (Fig. 69D). Clypeus medially with shallow but distinct longitudinal impression, surrounding surface with extremely shallow and obscure punctures. Terga impunctate. Restricted to northern Spain .... ***lathyri* Alfken**

– Pygidial plate apically rounded, never emarginate. Clypeus without medial impression, punctures usually clear. Terga with or without punctures.......**144**

144 Clypeus apically shiny. T2–4 apically with wide white hair bands that are complete in fresh specimens, these clearly exceeding the length of the marginal areas (Fig. 69E). Scutum laterally shagreened, becoming smooth and shiny medially. Restricted to the Sistema Central and northern and western Iberia ....***gredana*** **Warncke**

– Clypeus uniformly dull. T2–4 with hair bands different, either shorter, broadly interrupted medially, or yellowish (Fig. 69F). Scutum uniformly dull or with circular shiny area medially..**145**

145 Declivity of T1 medially strongly and densely punctate, punctures separated by <1 puncture diameter...**146**

– Declivity of T1 with at most scattered punctures, never with dense patch of punctures medially..**149**

146 T3 with interrupted apical hair band in fresh specimens. T2–4 with the apical hyaline part of the marginal areas narrow, not exceeding 3 times the diameter of a puncture from the tergal discs. Scutum uniformly dull. Restricted to northern Portugal and Spain with isolated populations at elevation in the Sistema Central and Sistema Ibérico .... ***wilkella*** **(Kirby)**

– T3 with apical hair band complete in fresh specimens (Fig. 69F). T2–4 with the apical hyaline part of the marginal areas comparatively broad, exceeding 4 times the diameter of a puncture from the tergal discs. Scutum at least partly shiny...**147**

147 Scutum shagreened laterally, medially with a circular area which is smooth and shiny; punctation here becoming weaker and sparser. Restricted to the Sistema Central to central and northern Portugal and north-western Spain (Zamora). Not known from the Cantabrian or Pyrenees Mountains........... .... ***benoisti*** **Wood & Praz**

– Scutum more or less uniformly shagreened and punctate. Found across mountainous areas in eastern Spain (Sierra Nevada, Sierra de Cazorla, Sistema Ibérico) to the Pyrenees..**148**

148 Restricted to the alpine zone of the Sierra Nevada (above 2000 m) .... ***contracta*** **Wood**

– Found elsewhere............................... ***intermedia*** **Thomson aggregate** (this likely represents a complex of an unknown number of species, potentially all of which are undescribed; the true *intermedia* may be absent from Spain)

149 Terga obscurely punctate, at least on the base of T2 with punctures disappearing into the underlying shagreenation. Univoltine (April–June) ... . ***russula*** **Lepeletier sensu lato** (including the distinct mitochondrial lineage from southern Portugal)

– Terga clearly punctate, at least on the base of T2 with punctures clearly visible against the underlying shagreenation...**150**

150 Terga strongly shagreened, dull to weakly shiny. Scutellum shagreened and weakly shiny. Tergal hair bands yellowish. Larger, 11–12 mm. Restricted

to southern and south-eastern Spain (Almería, Granada, Málaga, Murcia, Valencia). Univoltine (April–June) .... ***levante* Wood & Praz**

– Terga less strongly shagreened, shiny comparatively more strongly. Scutellum medially almost without sculpture, brightly shiny. Tergal hair bands whitish. Smaller, 8–10 mm. Throughout Iberia. Bivoltine (typically May–June; July–August) .... ***afzeliella* (Kirby)**

151 (138) Fovea dorsally narrow, occupying at most ⅓ of space between lateral ocellus and compound eye, ventrally narrowing strongly (subgenus *Euandrena*) **152**

– Foveae either dorsally broader, or not strongly narrowing **162**

152 Head elongate, mouthparts extremely long, twice the length of the head (c.f. Fig. 89D). Process of the labrum triangular. Associated with *Lithodora* (Boraginaceae) .... ***solenopalpa* Benoist**

– Head and mouthparts shorter, mouthparts never twice the length of the head. Process of the labrum trapezoidal **153**

153 Clypeus densely and coarsely punctate with a raised longitudinal impunctate shiny line. Restricted to areas close to the Pyrenees. Associated with *Symphytum* (Boraginaceae) .... ***symphyti* Schmiedeknecht**

– Clypeus densely or weakly punctate, never with a raised longitudinal impunctate shiny line **154**

154 Pronotum with weak but distinct lateral keel. Clypeus medially with shallow longitudinal impression **155**

– Pronotum laterally rounded. Clypeus without longitudinal impression, in one species (*A. rufula* Schmiedeknecht) with hints of an impression caused by impunctate longitudinal midline **156**

155 T2 with marginal area long, occupying almost ½ the segment, strongly depressed and shiny (Fig. 70A). Facial pubescence light brown, with at most dark hairs laterally on the frons. Terminal fringe brown. Found in areas with a temperate Atlantic climate across central, north-western, and northern Iberia .... ***angustior* (Kirby)**

– T2 with marginal area shorter, not strongly depressed (Fig. 70B). Face with intermixed black hairs throughout, including on the vertex (Fig. 8C). Terminal fringe dark brown to black (Fig. 8D). Found in areas with a Mediterranean climate .... ***lavandulae* Pérez**

156 Tergal discs with extremely coarse and dense punctures, punctures separated by 0.5–1 puncture diameter. Tergal margins strongly depressed and essentially impunctate, margins of T2–4 overlain by sparse whitish hair bands that emerge from the apexes of the tergal discs and which do not obscure the underlying surface of the marginal areas (Fig. 70C). Known only from mountainous areas in north-western, central, and south-eastern Spain (Léon, Ávila, Jáen) .... ***fortipunctata* Wood**

– Tergal discs with normal punctures, not noticeably coarse, punctures separated on average by 1 puncture diameter. Tergal margins only weakly depressed, without long whitish hair bands, sometimes with obscure brownish lateral hair bands on the apexes of the marginal areas themselves **157**

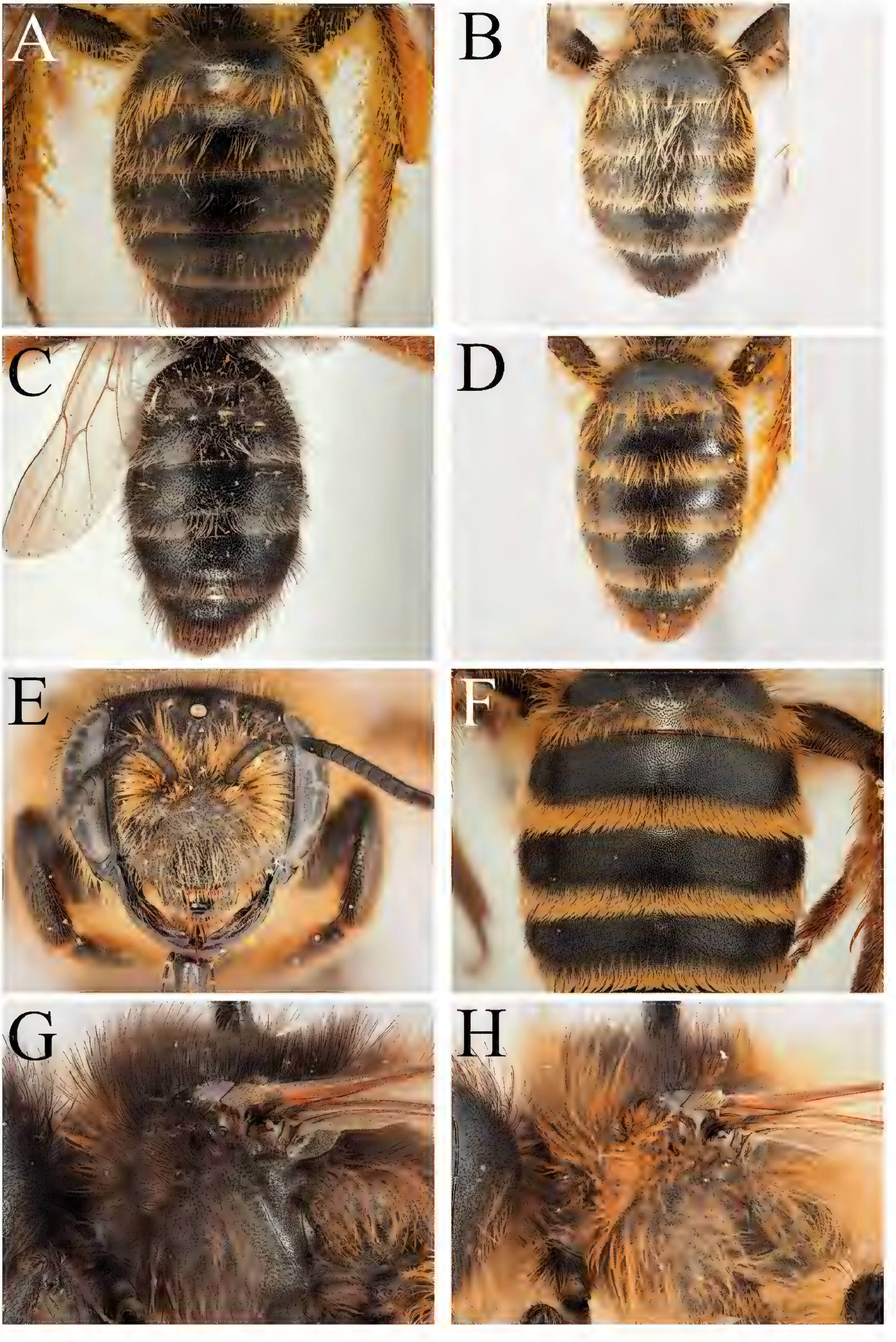

Figure 70. *Andrena* (*Euandrena*) *angustior* (Kirby, 1802), female **A** terga, dorsal view; *Andrena* (*Euandrena*) *lavandulae* Pérez, 1902, female **B** terga, dorsal view; *Andrena* (*Euandrena*) *fortipunctata* Wood, 2021, female **C** terga, dorsal view; *Andrena* (*Euandrena*) *granulosa* Pérez, 1902, female **D** terga, dorsal view; *Andrena* (*Melandrena*) *flavipes* Panzer, 1799, female **E** head, frontal view **F** terga, dorsal view; *Andrena* (*Melandrena*) *vulcana* Dours, 1873, female **G** mesosoma, profile view (dark form) **H** mesosoma, profile view (light form).

157 Apical margins of T1–4 extensively lightened yellow-hyaline, this lightened area clearly exceeding the diameter of a lateral ocellus (Fig. 70D). Associated with Cistaceae **158**

– Apical margins of T1–4 not extensively lightened yellow-hyaline, at most narrowly so, this lightened area not exceeding the diameter of a lateral ocellus **159**

158 Tergal margins comparatively more strongly depressed. Tergal discs on average more coarsely and densely punctate, punctures on the disc of T2 separated by 1.5–2 puncture diameters[15] .... ***granulosa* Pérez**

– Tergal margins comparatively more weakly depressed. Tergal discs on average less strongly and densely punctate, punctures on the disc of T2 separated by 3–4 puncture diameters[15] .... ***vulpecula* Kriechbaumer**

159 Facial pubescence predominantly light, with dark hairs restricted to the inner margins of the compound eyes. Mesepisternum entirely pale-haired. Restricted to temperate areas close to the Pyrenees .... ***rufula* Schmiedeknecht**

– Facial pubescence predominantly black, with occasional scattered light hairs (Fig. 48B). Mesepisternum with at least some black hairs (Fig. 48A), often with extensive dark pubescence **160**

160 Face long, majority of the clypeus passing below an imaginary line drawn between the ventral margins of the compound eyes. Clypeus comparatively sparsely punctate, punctures separated by an average of 1 puncture diameter, with impunctate longitudinal midline. Restricted to mountainous areas in northern and north-western Spain .... ***allosa* Warncke** (note, the Spanish taxon may be distinct from populations in Central Europe)

– Face short, only a small part of the clypeus falls below an imaginary line drawn between the ventral margins of the compound eyes. Clypeus comparatively densely punctate, punctures separated on average by 0.5–1 puncture diameter **161**

161 Clypeus extremely densely and coarsely punctate, punctures separated by 0.5 puncture diameters (Fig. 48B). Currently known only from the Sierra Nevada .... ***isolata* sp. nov.**

– Clypeus less densely punctate, punctures separated on average by 0.5–1 puncture diameters. Widespread across Iberia .... ***bicolor* Fabricius sensu lato** (two mitochondrial lineages are present in *A. bicolor*; to date, only the southern lineage has been found in Iberia)

162 (151) Clypeus punctate, interspaces forming weakly raised longitudinal wrinkles (Fig. 70E; former subgenus *Zonandrena*) **163**

– Clypeus without longitudinal wrinkles **167**

163 Face, mesepisternum, scutum anteriorly, and propodeum with abundant white hairs; scutum medially with contrasting short black pubescence.

15 These two species are very difficult to separate in the female sex. Association with males should be made where possible.

Marginal areas of T2–4 laterally with broad white hair patches that obscure the underlying surface. Restricted to steppic areas in central Spain...***soror* Dours**

– Face with pubescence variable, either black or a mixture of black and brown; if entirely white, then mesosoma with extensive brown pubescence dorsally. Terga with complete apical hair bands that are never interrupted medially in fresh specimens or with hair bands reduced and essentially absent **164**

164 Facial pubescence white. Rare, restricted to the Pyrenees ....***gravida* Imhoff**

– Facial pubescence black or a mixture of black and brown; never pure white **165**

165 Posterior face of hind femur with a latitudinal carina. Facial pubescence never entirely black, usually a mixture of yellow, brown, and black hairs, sometimes whitish. Terga usually with strong apical hair bands (Fig. 70F; beware abraded specimens). The most common and widespread Iberian *Andrena* species..***flavipes* Panzer**

– Posterior face of hind femur rounded, without a latitudinal carina. Facial pubescence dark, often entirely black (Fig. 11C), usually predominantly black with at most some intermixed dark brown hairs. Terga with hair bands variable, sometimes weakly present, sometimes almost entirely absent (Figs 11F, 12D). Generally rare and found in southern Iberia **166**

166 Propodeal triangle with finely raised rugae covering entire surface. Pubescence variable, from almost entirely melanic (Fig. 70G, with only the tibial scopa remaining orange-red) to light, with extensive brown hairs on the mesosoma and terga (Fig. 70H). Foveae comparatively weakly constricted medially. Usually with complete tergal bands present[16] ....***vulcana* Dours**

– Propodeal triangle with finely raised rugae covering only basal half, apical parts with fine granular shagreenation. Pubescence variable, but never entirely melanic, mesonotum always with at least some brown hairs (Figs 11D, 12B). Foveae comparatively strongly constricted medially. Tergal bands usually greatly reduced[16] ....***discors* Erichson**

167 (162) Dorsolateral surface of the propodeum reticulate, with large and shallow punctures (can be small in *A. nuptialis* Pérez), clearly contrasting the shagreened and shiny propodeal triangle, this lacking lateral carinae and becoming shinier on the declivity (Fig. 65H, often entirely shagreened in *A. nuptialis*). Pronotum lacking lateral keel. Clypeus typically weakly to moderately domed, densely punctate (punctures separated by 1 puncture diameter, with more or less pronounded impunctate midline (subgenus *Hoplandrena*) **168**

– Without this combination of characters, pronotum keeled or not.........**173**

168 Hind tibiae and/or tarsi golden-orange...**169**

– Both hind tibiae and tarsi dark, at most obscurely reddish-brown.........**170**

16 These two species are difficult to separate due to enormous colour variation.

169 Hind tibiae golden-orange. Clypeus medially with a clearly raised longitudinal impunctate area, this area smooth and shiny, strongly contrasting the remaining parts of the clypeus which are densely punctate. Northern and central Spain, in areas with deciduous forest. Associated with *Quercus* (Fagaceae) .... ***ferox* Smith**

– Hind tibiae dark. Clypeus with faint impunctate longitudinal line medially, but this is not raised and not shiny, therefore not strongly contrasting with the remaining parts of the clypeus which are regularly punctate. Rare, restricted to the Pyrenees .... ***bucephala* Stephens**

170 A3 clearly exceeding length of A4+5 .... ***nuptialis* Pérez**

– A3 not clearly exceeding length of A4+5, usually as long as or slightly shorter than A4+5.. **171**

171 Metasomal terga with short hairs, most clearly seen in profile on T2–3 with hairs not exceeding width of a flagellum....... ***rosae* Panzer** (*partim*, dark form)

– Metasomal terga with extensive and abundant long hairs, most clearly seen in profile on T2–3 with hairs clearly exceeding width of a flagellum............. **172**

172 Tibial scopa in fresh specimens usually dark dorsally and silver ventrally. Usually with light brown facial hair. Usually univoltine, flying April to mid-June, with potential sporadic emergence in August and September (not yet observed in Iberia). Rare, restricted to cooler parts of Iberia[17] .... ***scotica* Perkins**

– Tibial scopa in fresh specimens dark dorsally and golden ventrally, but this can be ambiguous and fade to silver in older specimens or pinned material. Facial hair can be dark, particularly in the spring generation, the summer generation usually has lighter facial hair. Bivoltine, usually flying March–May and July–August, with phenology depending on local conditions. Common and widespread across Iberia[17] .... ***trimmerana* (Kirby)** (*partim*, dark form)

173 (167) Pronotum laterally keeled, angulate, keel runs up dorsally to an angled corner.. .... **174**

– Pronotum laterally rounded, without a keel **205**

174 Mesepisternum deeply and distinctly punctate, punctures separated by <1 puncture diameter, with weakly shiny interspaces. Ocelloccipital distance exceeding 3 times the diameter of a lateral ocellus. Terga extremely densely punctate, punctures separated by <0.5 puncture diameters, with shiny interspaces. No recent records, possibly extinct, restricted to central Spain......... .... ***incisa* Eversmann**

– Without this combination of characters, mesepisternum usually impunctate or only obscurely punctate, ocelloccipital distance shorter, terga dull or less densely punctate **175**

17 These two species cannot be consistently morphologically separated with confidence. Association with males should be made. See discussion and notes in Wood et al. (2022c).

175 Fore margin of clypeus slightly upturned, forming wide] shape, dorsolateral surface of propodeum reticulate, impunctate, not strongly differentiated from the propodeal triangle, terga with dense apical hair bands on T2–4, fovea broad and occupying over ½ of the distance between the compound eye and the lateral ocellus, tibial scopae with hairs long and loose. Restricted to central, southern, and eastern Spain and associated with *Reseda* (Resedaceae) **176**

– Without this combination of characters **177**

176 Terminal fringe orange. Tibial scopae orange. Tergal discs with extremely fine shagreen, shiny, clearly and deeply punctate .... ***relata* Warncke**

– Terminal fringe dark brown medially and white laterally (Fig. 40D). Tibial scopae white (Fig. 40A). Tergal discs strongly shagreened, weakly shiny, obscurely and shallowly punctate (Fig. 40D) .... ***blanda* Pérez**

177 Pygidial plate flat to weakly convex, outer margin usually somewhat elevated, without clearly raised area medially (Fig. 71A; subgenus *Notandrena partim*) **178**

– Pygidial plate with distinctly limited raised area medially (Fig. 71B) **186**

178 Scutum with very dense and even punctation across the entire surface of the disc, punctures separated by much less than the diameter of a puncture, in some cases nearly touching (Fig. 57C). Underlying integument strongly shagreened and dull .... ***griseobalteata* Dours**

– Scutum with moderate and uneven punctation, punctures separated by 1–3 puncture diameters in some cases. If occasional punctures are close to touching, then this is not consistently replicated across the whole scutum, with other punctures being separated by a clear distance. Underlying integument variable, from shagreened to shiny **179**

179 Hind tibia and all tarsi completely orange. Restricted to areas close to the Pyrenees... ***chrysosceles* (Kirby)**

– Hind tibia black, tarsi may be black or orange **180**

180 Larger species, body length 11–12 mm. T2–4 with thick white apical hair bands that obscure the underlying surface, only weakly interrupted medially on T2 .... ***langadensis albipila* Warncke**

– Smaller species, body length 7–10 mm. T2–4 usually with weaker hair bands **181**

181 Tibial scopa, when viewed in reverse profile (i.e. looking at the posterior face of the hind tibia) dorsally short and thick, hair length only 1–1.5 times the diameter of a lateral ocellus, clearly shorter than the ventral scopal hairs. Restricted to areas close to the Pyrenees .... ***pallitarsis* Pérez**

– Tibial scopa equally long dorsally and ventrally **182**

182 Terga very sparsely punctate, punctures of discs of T2–4 shallow, obscure, and separated by 3–4 puncture diameters. Clypeus comparatively flattened. Very rare, known only from southern Spain (Cádiz)................ ***microthorax* Pérez**

– Terga densely punctate, punctures on discs of T2–4 strong and deep, separated at most by 2 puncture diameters, usually by <2 puncture diameters. Clypeus comparatively domed **183**

Figure 71. *Andrena* (*Notandrena*) *griseobalteata* Dours, 1872, female **A** pygidial plate, posterior view; *Andrena* (*Leucandrena*) *leptopyga* Pérez, 1895, female **B** pygidial plate, posterior view; *Andrena* (*Notandrena*) *foeniculae* Wood, 2020, female **C** head, dorsal view; *Andrena* (*Notandrena*) *nitidiuscula* Schenck, 1853, female **D** head, dorsal view **E** scutum, dorsolateral view; *Andrena* (*Notandrena*) *fulvicornis* Schenck, 1861, female **F** scutum, dorsolateral view.

183 Vertex clearly elongate, the hind ocelli separated from the margin of the vertex by a distance greater than the diameter of a lateral ocellus (Fig. 71C). Genae enlarged so that the hind margin of the vertex forms a weak U-shape .... ***foeniculae* Wood**

– Vertex not elongate, the hind ocelli separated from the margin of the vertex by a distance clearly less than the diameter of a lateral ocellus (Fig. 71D). Hind margin of the vertex in comparison almost straight **184**

184 Central line in the front half of the scutum strongly impressed (Fig. 71E). Restricted to temperate habitats in northern Iberia. Hind basitarsi dark. Univoltine (July–August) .... ***nitidiuscula* Schenck**

– Central line in the front half of the scutum only weakly and superficially impressed (Fig. 71F). Hind basitarsi dark to often entirely lightened orange. Not restricted to northern Iberia, and active in the spring or the summer.......... **185**

185 Disc of T1 densely punctate, punctures separated by 1 puncture diameter. Scutellum shagreened and dull. Hind basitarsi orange. Throughout Iberia. Bivoltine (March–August) .... ***fulvicornis* Schenck**

– Disc of T1 sparsely punctate, punctures separated by 2–3 puncture diameters. Scutellum polished and shiny. Restricted to strongly saline habitats in southern Iberia. Voltinism unclear, possibly bivoltine, recorded March–early June.. ***juliana* Wood**

186 Flying exclusively in the summer (July–September). Hind tibiae triangular, clearly much broader apically than basally, with short scopal hairs not greatly exceeding the diameter of a lateral ocellus (Fig. 72A). Terga with strong and broad apical tergal hair bands (Fig. 72B; subgenus *Cnemidandrena* Hedicke).. **187**

– Flying predominantly in the spring, some species extending into July. Hind tibiae normal, not greatly broader apically than basally, with long scopal hairs, clearly greatly exceeding the diameter of a lateral ocellus. Terga with or without clear apical hair bands **189**

187 Outer surface of the galea smooth and shiny. Associated with Ericaceae, found in Atlantic habitats across northern, central, and western Iberia........ .... ***fuscipes* (Kirby)**

– Outer surface of the galea shagreened and dull..................................... **188**

188 Mesosoma anteriorly and posteriorly with pale hairs, medially with abundant black hairs. Face with pale hairs. Associated with Asteraceae, restricted to northern Spain .... ***denticulata* (Kirby)**

– Mesosoma with pale to brown hairs, with at most occasional intermixed black hairs. Face black-haired. Polylectic, though often found on Asteraceae. Restricted to areas surrounding the Pyrenees and the Cantabrian Mountains with isolated populations in high mountains in southern Spain (particularly the Sierra Nevada) .... ***nigriceps* (Kirby, 1802)**

189 Process of the labrum either elongate (as long as or slightly longer than broad) or pointed triangular, never medially emarginate (Fig. 72C–H). Clypeus sometimes with transverse wrinkles (subgenus *Leucandrena*)............................ **190**

– Process of the labrum trapezoidal, always broader than long, usually medially emarginate, at least weakly. Clypeus never with transverse wrinkles (subgenus *Andrena* s. str.).. **197**

190 Fovea very wide, occupying the entirety of the space between the inner margin of compound eye and the lateral ocellus.. **191**

– Fovea narrower, occupying between half and two-thirds of distance between the inner margin of compound eye and the lateral ocellus..................... **192**

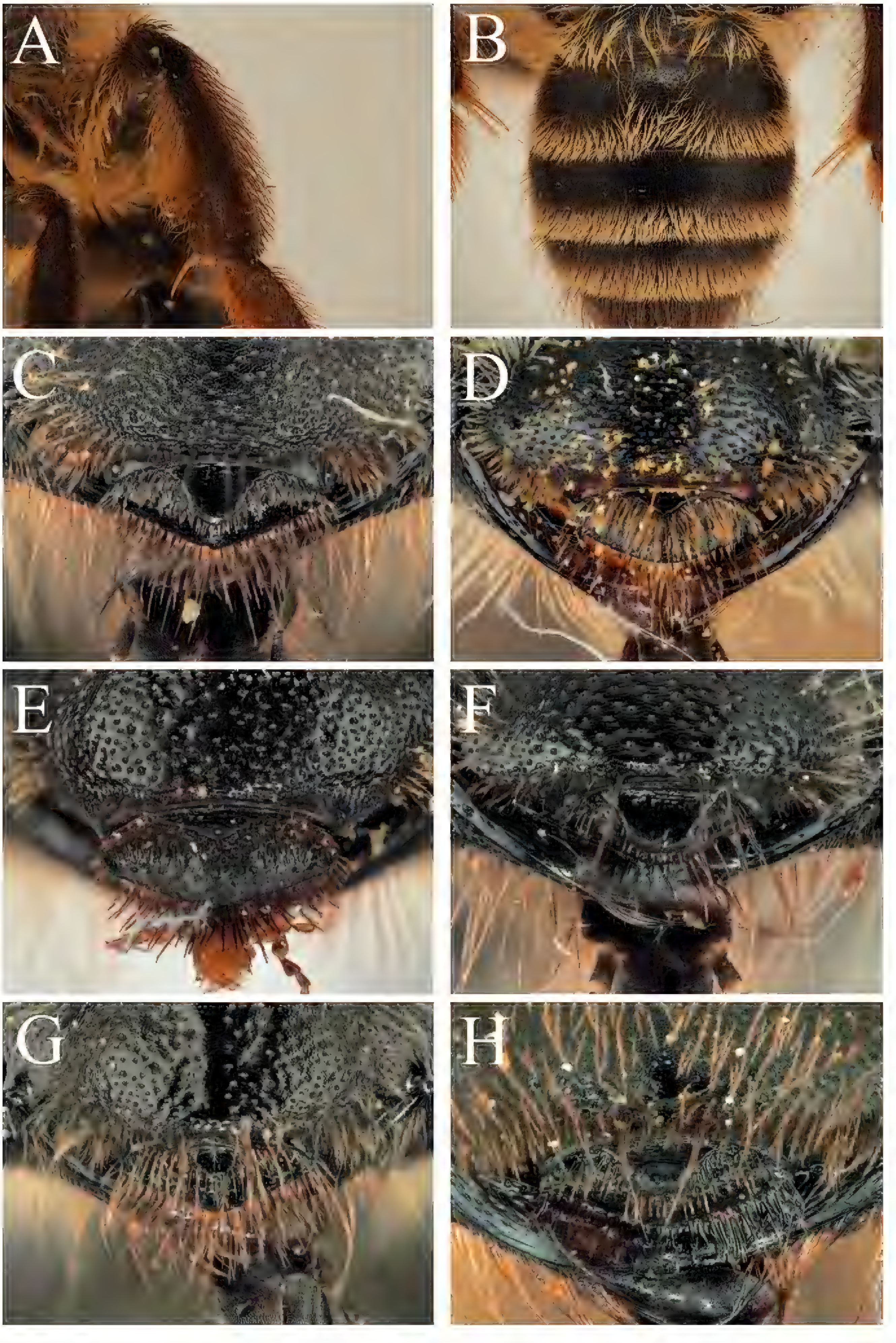

Figure 72. *Andrena* (*Cnemidandrena*) *denticulata* (Kirby, 1802), female **A** hind leg, profile view **B** terga, dorsal view; *Andrena* (*Leucandrena*) *barbilabris* (Kirby, 1802), female **C** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *tunetana* Schmiedeknecht, 1900, female **D** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *sericata* Imhoff, 1868, female **E** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *parviceps* Kriechbaumer, 1873, female **F** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *ventralis* Imhoff, 1832, female **G** process of the labrum, frontal view; *Andrena* (*Leucandrena*) *leptopyga* Pérez, 1895, female **H** process of the labrum, frontal view.

191 Clypeus with network of fine, raised ridges that extend laterally across the disc, underlying surface shiny. Process of labrum short, broader than long, produced to a fine triangular point (Fig. 72D) .... ***tunetana* Schmiedeknecht**

– Clypeus without any lateral ridges, underlying surface shagreened, dull. Process of labrum short and slightly broader than long, but clearly trapezoidal, apical margin slightly thickened and raised (Fig. 72H) ...... ***leptopyga* Pérez**

192 Scutum and scutellum shagreened, dull. Process of labrum as long as broad, evenly rounded apically (Fig. 72C) .... ***barbilabris* (Kirby)**

– At least some part of the scutum or scutellum shiny. Process of labrum either pointed triangular or apically truncate, not evenly rounded apically........... **193**

193 Process of labrum pointed triangular (Fig. 72E). Very rare, restricted to the Pyrenees.. ***sericata* Imhoff**

– Process of labrum apically truncate, not pointed (Fig. 72F, G) **194**

194 Terga clearly finely and densely punctured, punctures separated by 1–2 puncture diameters, visible against weakly shagreened integument. Restricted to mountainous areas of central and northern Spain .... ***argentata* Smith**

– Terga with punctures sparse and difficult to see, separated by 3–5 puncture diameters **195**

195 Process of labrum comparatively large, apex more rounded (Fig. 72F). Fovea, viewed dorsally, with dark brown hairs. Terminal fringe dark brown. Larger, 10–11 mm .... ***parviceps* Kriechbaumer**

– Process of labrum comparatively small, more clearly truncate (Fig. 72G). Fovea, viewed dorsally, with light brown hairs. Terminal fringe golden. Smaller, 7–9 mm **196**

196 Scutum shagreened laterally, but centrally shagreenation is absent, underlying surface therefore smooth and shiny. Lateral faces of the propodeum with clearly raised more or less parallel ridges. Scutum more strongly punctured, individual punctures larger and closer together, particularly anteriorly where they are separated by 1–2 puncture diameters .... ***dinizi* Warncke**

– Scutum shagreened, shagreenation weaker centrally but still clearly visible. Lateral faces of the propodeum with at most very small wrinkles. Scutum less strongly punctured, individual punctures normal and more scattered, separated by 1–3 puncture diameters .... ***ventralis* Imhoff**

197 Terga densely covered with long hairs, in fresh specimens these obscuring the underlying surface (Fig. 73A)...**198**

– Terga less thickly haired, sometimes with hair tufts on T1–2, but these not obscuring the underlying surface (Fig. 73B)..**199**

198 Hind tibiae orange. Terga predominantly black-haired, sometimes with light brown hairs on T1. Restricted to northern Spain, associated with *Salix* (Salicaceae) .... ***clarkella* (Kirby)**

– Hind tibiae dark. Terga 1–5 with extensive reddish-orange pubescence (Fig. 73A). With a patchy distribution from northern Portugal and Spain to the Pyrenees, with an isolated population in the Sierra de Cazorla (Jáen). Associated with various flowering trees and shrubs.............. ***fulva* (Müller)**

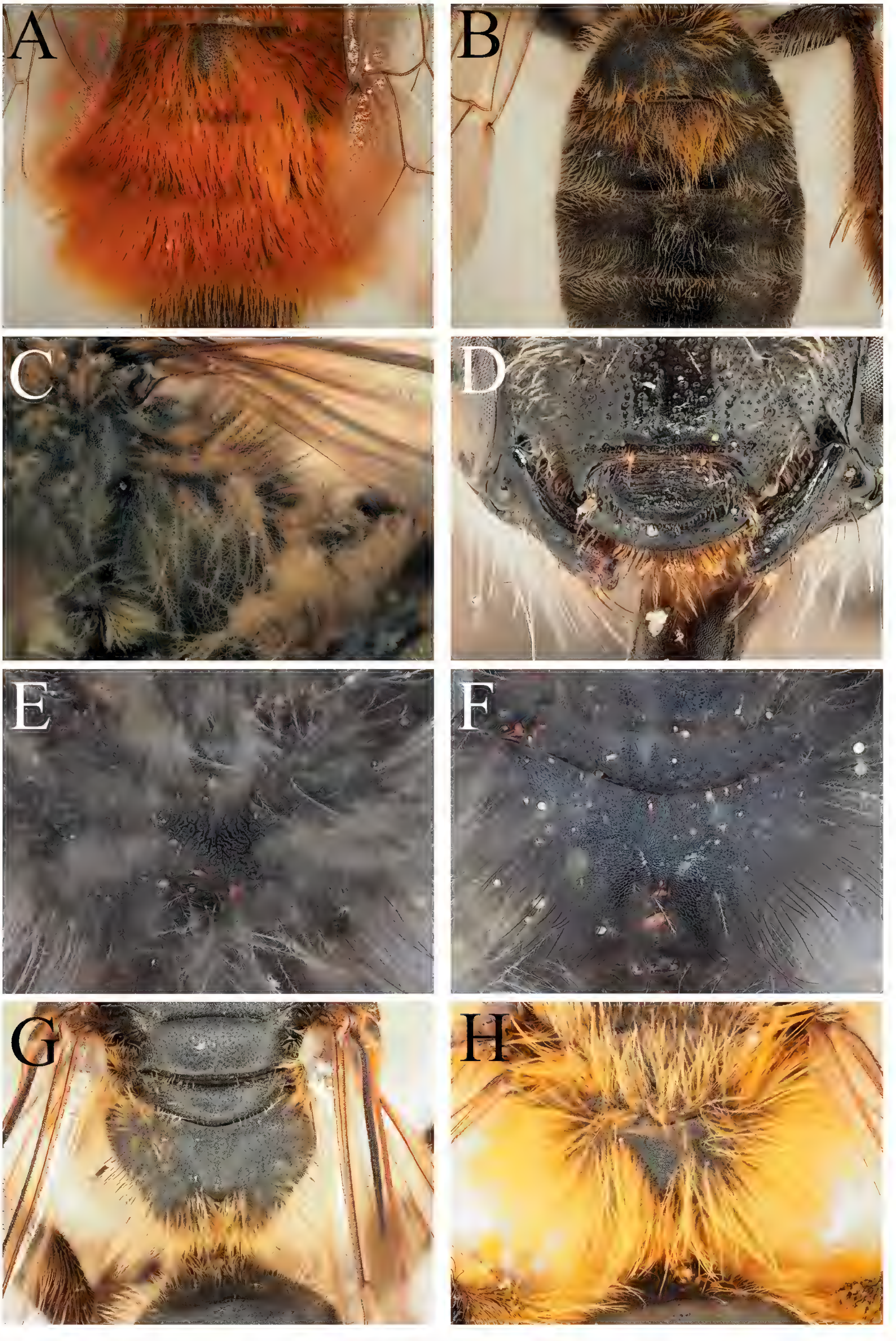

Figure 73. *Andrena* (*Andrena*) *fulva* (Müller, 1776), female **A** terga, dorsal view; *Andrena* (*Andrena*) *helvola* (Linnaeus, 1758), female **B** terga, dorsal view; *Andrena* (*?Euandrena*) *ramosa* Wood, 2022, female **C** propodeal corbicula, profile view; *Andrena* (*Didonia*) *mucida* Kriechbaumer, 1873, female **D** process of the labrum, ventral view; *Andrena* (*Avandrena*) *erodiorum* Wood & Ortiz-Sánchez, 2022, female **E** propodeum, dorsal view; *Andrena* (*Avandrena*) *melacana* Warncke, 1967, female **F** propodeum, dorsal view; *Andrena* (*Nobandrena*) *funerea* Warncke, 1975, female **G** propodeum, dorsal view; *Andrena* (*Truncandrena*) *ferrugineicrus* Dours, 1872, female **H** propodeum, dorsal view.

199 Marginal areas of T2–4 very wide, occupying ¾ of each segment .... ***synadelpha*** **Perkins**

– Marginal areas of T2–4 never occupying more than ½ of each segment, usually covering only ⅓ **200**

200 Face with entirely pale hairs, at most with a few scattered dark hairs along the inner margin of the compound eye **201**

– Face with extensive black hairs, particularly around the antennal insertions and along the inner margin of the compound eye **203**

201 Terga sparsely haired, with at most weak hair tufts on T1–2. Terga finely shagreened and thus weakly shiny. Restricted to northern Spain. Flying later in the year (June–August), associated with shrubs, particularly *Rubus* (Rosaceae) .... ***fucata*** **Smith**

– Terga typically with long hairs, in fresh specimens with clear and dense hair tufts on T1–2. Abraded or older specimens may lack such hair tufts, in which case use the following characters: terga strongly shagreened, dull. Flying earlier in the year (March–May), associated with flowering trees **202**

202 Basitarsi of hind tibiae parallel-sided, not converging apically. Restricted to the Pyrenees with an isolated population in the Sierra de Cazorla (Jáen). Associated with various flowering trees and shrubs .... ***helvola*** **(Linnaeus)**

– Basitarsi of hind tibiae broader basally, narrower apically, therefore converging apically. Restricted to areas around the Pyrenees and the Cantabrian Mountains. Associated with *Salix* (Salicaceae) .... ***mitis*** **Schmiedeknecht**

203 Face entirely black haired, without any pale hairs. Terga basally (T1–2) with orange-brown hairs, apically (T3–4) with extensive and strongly contrasting black hairs. Associated with *Vaccinium* (Ericaceae) .... ***lapponica*** **Zetterstedt**

– Face with at least some pale hairs, particularly around the antennal insertions. Terga without extensive areas with black hairs, generally with mixture of predominantly yellowish to brownish hairs on T1–4. Species associated with *Salix* (Salicaceae) **204**

204 Smaller, 10–11 mm. Clypeus predominantly shagreened and dull, with only the narrow longitudinal impunctate midline weakly shiny. Terminal fringe dark brown .... ***praecox*** **(Scopoli)**

– Larger, 11–14 mm. Clypeus comparatively shinier, only laterally shagreened and dull, apico-medially broadly shiny around the comparatively broader longitudinal impunctate midline. Terminal fringe black............. .... ***apicata*** **Smith**

205 (173) Large species (over 12 mm in length). With abundant black, brown, and/or white pubescence. Clypeus strongly domed. Ocelloccipital distance long, at least 2 times the diameter of a lateral ocellus (subgenus *Melandrena partim*) **206**

– Without this combination of characters; remaining species................... **212**

206 Tergal discs T1–3(4) with upstanding mixture of short pale whitish to light brown hairs extending over both disc and marginal areas. Tibial scopae orange-red, or bicoloured and dorsally dark, ventrally orange (dark form, active February-April). Terga sometimes with greasy-bronzy metallic reflections .... ***nigroaenea* (Kirby)**

– Tergal discs never with this sort of pubescence, sometimes with white to brownish pubescence in basolateral corners of tergal discs, never extending onto marginal areas. Tibial scopae entirely black or a combination of black and white, never orange-red. Terga dark, without metallic reflections.......................... **207**

207 Mesosoma with black and white hairs, never with brown hairs **208**

– Mesosoma with black, brown, and/or pale hairs, never with only black and white hairs **209**

208 T2–4 laterally with thick apical patches of white hairs, these strongly contrasting the black integument .... ***albopunctata* (Rossi)**

– T2–4 laterally without white hair patches, entirely dark......... ***morio* Brullé**

209 Tibial scopae bicoloured, black dorsally and white ventrally. Mesosoma dorsally with bright orange-brown pubescence, laterally with pale pubescence, never with black hairs on the mesepisternum. Univoltine, flying April-June. Restricted to temperate parts of northern Spain .... ***nitida* (Müller)**

– Tibial scopae entirely black. Mesosoma dorsally usually with the pubescence darker, laterally with pubescence never pale, usually with abundant black hairs, at most with pubescence of the mesepisternum brown **210**

210 Disc of T1 shagreened and barely punctate, punctures scattered and obscure against the underlying sculpture........................... ***assimilis* Radoszkowski**

– Disc of T1 polished and shiny, strongly punctate, punctures clearly visible against the underlying sculpture.. **211**

211 Disc of T1 with punctures comparatively sparse, separated by 2 puncture diameters .... ***thoracica* (Kirby)**

– Disc of T1 with punctures dense, punctures separated by up to 1 puncture diameter, often separated by less .... ***limata* Smith**

212 (205) Propodeal corbicula complete, with both anterior and dorsal fringe, fringes composed of long, dense, and extremely plumose yellowish-brown hairs, these plumose hairs present also on the mesepisternum, the flocculus, and the femoral scopae (Fig. 73C), but hairs of the tibial scopae simple (see also illustrations in Wood et al. 2022). Known only from south-western Spain (Cádiz, Sevilla), flying in the very early spring (January–March) .... ***ramosa* Wood**

– Propodeal corbicula simple, composed of simple or weakly plumose hairs, but if plumose then these not extending onto the mesepisternum, flocculus, and femoral scopae **213**

213 Process of the labrum large, as long as broad, apically rounded, ventral surface covered with latitudinal wrinkles (Fig. 73D). Fovea narrow, occupying slightly less than half the space between the compound eye and the lateral

ocellus. Associated with *Muscari* (Asparagaceae).. ....***mucida* Kriechbaumer** (*partim*, 1st generation)

– Process of the labrum different, either wider than long, trapezoidal, or apically pointed, ventral surface never covered with latitudinal wrinkles. Foveae narrow or broad..**214**

214 Head short and broad, at least 1.3 times wider than long. Fovea short and broad, only slightly longer than wide. Small bees, 8–10 mm, with long white pubescence in fresh specimens. Associated with *Erodium* (Geraniaceae)..... **215**

– Without this combination of characters, usually larger. Never associated with *Erodium*...**217**

215 Propodeum and mesepisternum entirely microreticulate, without strong or weak raised network of reticulation (Fig. 73F). Mesepisternum laterally with extensive intermixed black and white hairs. Terga with sparse and short pubescence, T2–4 with only weak apical hair bands that do not obscure the underlying surface. Known from across southern Spain (Albacete, Cádiz, Granada, Málaga) .... ***melacana* Warncke**

– Propodeum and mesepisternum shiny or with granular microreticulation, overlain by strong or weak network of raised rugosity (Figs 47E, 73E). Mesepisternum predominantly pale-haired, at most with 30% of hairs black. Terga with long erect white hairs, forming dense apical hair bands on T2–4 which obscure the underlying surface (Fig. 47F). Known from either south-eastern (Albaceae) or south-western (Cádiz) Spain **216**

216 Propodeum (including propodeal triangle) and mesepisternum with strongly produced but fine interlinked network of raised rugosity (Fig. 73E). Facial foveae occupying ¾ of space between the compound eye and a lateral ocellus. Apical fringe of T5 and hairs flanking pygidial plate golden-brown. Known from south-eastern Spain (Albacete) .... ***erodiorum* Wood & Ortiz-Sánchez**

– Propodeum with fine granular shagreen, with weak network of raised rugosity, propodeal triangle slightly depressed, basal 2/3rds with raised longitudinal rugae (Fig. 47E). Facial foveae occupying ½ space between the compound eye and a lateral ocellus (Fig. 47C). Apical fringe of T5 and hairs flanking pygidial plate dark brown (Fig. 47F). Known from south-western Spain (Cádiz)...***juliae* sp. nov.**

217 Terga shagreened and dull, impunctate or with obscure and scattered punctures (Figs 30D, 39D, 51C)..**218**

– Terga polished and shiny, at most finely shagreened, clearly and densely punctate..**227**

218 Propodeal triangle with internal surface covered with fine network of raised reticulation **219**

– Propodeal triangle with internal surface smooth, entirely granularly shagreened, without raised reticulation (Fig. 73G, H)...............................**220**

219 Mid and hind basitarsi dark. Tergal discs in profile view with sparse and short dark hairs, apically with white hair bands. Throughout Iberia .... ***hypopolia* Schmiedeknecht**

– Mid and hind basitarsi orange (Fig. 39B). Tergal discs in profile view laterally with orange hair, apically with long yellowish hair bands (Fig. 39D). Restricted to high altitude sites (>1200 m) in the Pyrenees ....***ranunculorum* Morawitz**

220 Propodeum with comparatively few hairs, these largely restricted laterally to the dorsal fringe of the propodeal corbicula, propodeum dorsally with sparse pubescence (Fig. 73G). Process of the labrum narrow, only slightly broader than long, more or less triangular with a rounded apex. Dorsolateral surfaces of the propodeum obscurely and shallowly punctate. T2–4 with narrow white apical hair bands. Terminal fringe bright orange. Restricted to central Spain...***funerea* Warncke**

– Propodeum covered with long abundant pubescence, no meaningful difference between hairs of the dorsal fringe of the propodeal corbicula and those on the dorsal surface of the propodeum (Fig. 73H). Process of the labrum usually trapezoidal, broader than long, with or without an emarginate front margin. If unclear, then dorsolateral surfaces of the propodeum clearly and coarsely punctate. T2–4 with or without hair bands. Terminal fringe darker, from light brown to dark brown or almost black (subgenus *Truncandrena*)... **221**

221 T2–4 with clear apical hair bands **222**

– Terga without apical hair bands, hairs may be present on the tergal discs **224**

222 Fovea relatively narrow, occupying ½ the space between the compound eye and the lateral ocellus. Process of the labrum triangular, slightly truncate. Smaller, not exceeding 10 mm in length. Associated with Brassicaceae........ ....***medeninensis donata* Warncke**

– Fovea broad, occupying ¾ of space between the compound eye and the lateral ocellus. Process of the labrum trapezoidal with a strong emargination medially. Larger, exceeding 12 mm in length. Associated with *Cistus* (Cistaceae) **223**

223 Scopa bicoloured, black dorsally and orange ventrally (Fig. 51D). Face longer, clypeus ventrally projecting well below a line drawn between the lower margins of the compound eyes (Fig. 51B). Larger, 15–16 mm. Known only from southern Spain (Málaga) ....***ghisbaini* sp. nov.**

– Scopa unicolourous orange (Fig. 30B). Smaller, 12–13 mm. Face shorter, clypeus only slightly projecting below a line drawn between the lower margins of the compound eyes (Fig. 30C). Throughout Iberia ....***villipes* Pérez**

224 Mid and hind basitarsi entirely lightened orange..................................**225**

– Mid and hind basitarsi dark, at most obscurely dark reddish.................**226**

225 Mesepisternum laterally with abundant dark hairs. Base of discs of T2–4 strongly depressed (depressed relative to the apical margin of the preceding tergum, often with a physical space between them), this depression therefore laterally exaggerating the gradulus along its inner margin. Tergal margins (and sometimes sides of terga when viewed laterally) sometimes lightened reddish, contrasting the dark discs. Rare, known only from southern Spain (Alicante, Cádiz) .... ***minapalumboi* Gribodo**

– Mesepisternum laterally with entirely pale hairs. Base of T2–4 not noticeably depressed, therefore gradulus not particularly noticeable. Tergal margins always dark. Common throughout Iberia ....***ferrugineicrus* Dours**

226 Discs of T2–4 with abundant and extensive pale pubescence, in fresh specimens this pubescence forming distinct patches laterally. Marginal areas broad, on T3–4 occupying $^2/_5$ of the length of the segment. Clypeus shagreened and dull, with a narrow impunctate longitudinal mid line, only slightly shiny at extreme apex. Throughout Iberia.................................. ***nigropilosa* Warncke**

– Discs of T2–4 with at most scattered and fine hairs, never forming patches. Marginal areas narrow, on T3–4 occupying at most $1/5^{th}$ of the length of the segment. Clypeus less extensively shagreened and dull, becoming smooth and shiny in its apical half, with broader impunctate longitudinal mid line. Rare, known only from southern Spain (Córdoba) .... ***varia* Pérez**

227 Terga without apical hair bands, or with obscure hair bands that are widely interrupted medially even in fresh specimens (Fig. 74A, B). Tibial scopae bicoloured, dark dorsally and white ventrally. Terminal fringe dark brown to black, with some white hairs laterally...**228**

– Terga with clear apical hair bands, these complete at least on T3–4 (Fig. 74C, E, F). Tibial scopae unicolourous white or golden-orange. Terminal fringe light, reddish-brown to golden..**229**

228 Terga with widely interrupted apical hair bands, often abraded and absent. Terga coarsely and densely punctate, tergal margins strongly depressed, with punctures at most half the size of those on the tergal discs (Fig. 74A). Rare, restricted to southern Iberia .... ***macroptera* Warncke**

– Terga without apical hair bands. Terga extremely finely punctate, no major difference in the size of the punctures on the weakly depressed marginal areas compared to the discs (Fig. 74B). More widespread across southern, central, and eastern Iberia .... ***corax* Warncke**

229 Scutum sparsely punctate, punctures separated by 1–2 puncture diameters, laterally shagreened and dull, shagreenation weakening medially and on the scutellum, here shiny. Process of the labrum short and triangular (Fig. 74D)... ***urdula* Warncke**

– Scutum and scutellum densely punctate, punctures separated by up to 1 puncture diameter, underlying surface uniformly finely shagreened and weakly shiny. Process of the labrum trapezoidal, margin truncate to weakly emarginate... **230**

230 Tergal discs extensively covered with extremely short hairs, forming a velvety pubescence in addition to denser and longer hairs on tergal margins, almost obscuring the underlying surface in fresh specimens (Fig. 74E). Mesosoma dorsally with whitish-brown pubescence. Tibial scopae white. Terminal fringe whitish-orange overlain by white hairs. Associated with small-flowered Fabaceae (*Lotus*) .... ***farinosa*** **Pérez**

– Tergal discs with scattered short orange hairs, not forming a velvety pubescence (Fig. 74F). Mesosoma dorsally with rich orange-brown pubescence. Tibial scopae and terminal fringe uniformly orange. Associated with *Reseda* (Resedaceae) .... ***murana*** **Warncke**

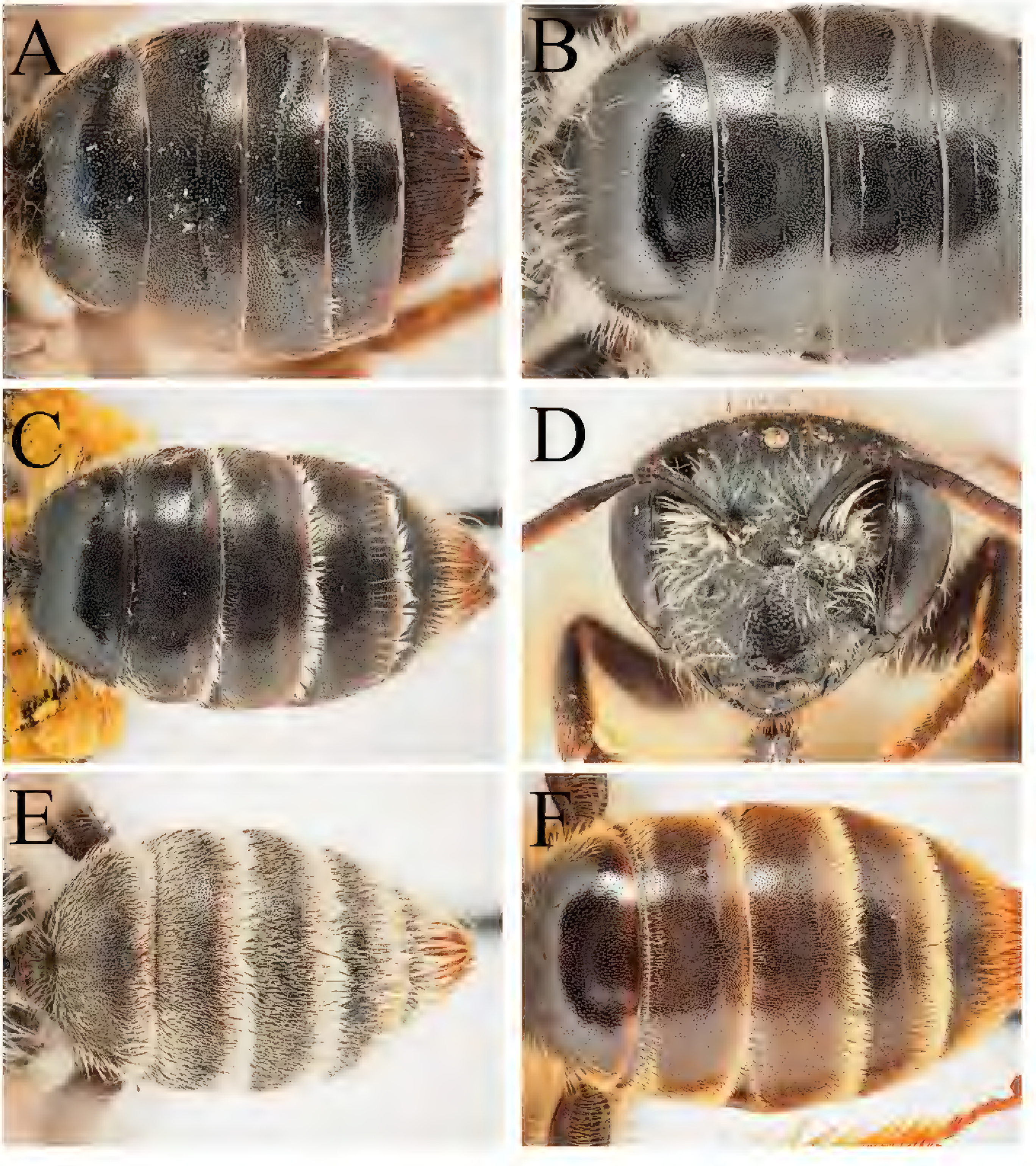

Figure 74. *Andrena* (incertae sedis) *macroptera* Warncke, 1974, female **A** terga, dorsal view; *Andrena* (incertae sedis) *corax* Warncke, 1975, female **B** terga, dorsal view; *Andrena* (incertae sedis) *urdula* Warncke, 1965, female **C** terga, dorsal view **D** face, frontal view; *Andrena* (*Ovandrena*) *farinosa* Pérez, 1895, female **E** terga, dorsal view; *Andrena* (incertae sedis) *murana* Warncke, 1975, female **F** terga, dorsal view.

For the male key, the following shortcuts can be used:

A. Clypeus at least partly yellow-marked.. **go to 2**

B. Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate .... **go to 52**

C. Genital capsule distinctive, with clear 90° emargination in the outer parts of the gonostyli. The most common *Andrena* species in Iberia................................... .... **go to *Andrena flavipes* Panzer**

D. Process of the labrum thickened and expanded, anteriorly projecting beyond the fore margin of the clypeus. Pronotum with strong humeral angle. Active in the summer (mid-June to September) (subgenus *Cnemidandrena* and remaining *Margandrena*)... **go to 68**

E. Fore margin of clypeus upturned AND gena conspicuously broadened, wider than the width of the compound eye AND pronotum with a conspicuous humeral angle (remaining *Notandrena*).. **go to 72**

F. Small species, body length of 5–7 mm (exceptionally 8 mm), terga always dark (remaining *Aciandrena*, *Aenandrena partim*, *Avandrena*, *Cordandrena*, *Cryptandrena partim*, *Graecandrena*, and almost all *Micrandrena*) .... **go to 77**

G. Mesepisternum and/or dorsolateral parts of the propodeum conspicuously punctate AND ocelloccipital distance at least 3 times the diameter of a lateral ocellus (*incisa*-group, *Pruinosandrena*) .... **go to 122**

H. Clypeus flattened over majority of its surface (subgenus *Taeniandrena*) .... **go to 127**

I. At least some tergal discs red-marked .... **go to 140**

J. Tergal discs with metallic blue reflections .... **go to 145**

K. Mandibles elongate, sickle-like, strongly crossing apically. Pronotum with strong humeral angle. Gena often expanded, broader than the width of a compound eye .... **go to 148**

L. Measured along ventral margin, A3 twice as long as A4..................... **go to 168**

M. Measured along ventral margin, A3 shorter than or as long as A4 .... **go to 194**

N. Remaining species; measured along ventral margin, A3 slightly longer than A4 .... **go to 215**

Males

1 Clypeus at least partly yellow-marked (Figs 44D, 75A–F); marking may be reduced to small marking medially or apically.. **2**

– Clypeus entirely dark, never with yellow markings................................. **51**

2 Clypeus and lower paraocular areas with yellow markings; paraocular markings may be reduced to small spots (Fig. 75A–C)...................................... **3**

– Yellow facial markings restricted to the clypeus, paraocular areas entirely dark (Figs 44D, 75D–F) **15**

3 Propodeum almost entirely declivous, without clearly differentiated horizontal and vertical parts. Propodeum with dorsolateral parts adjacent to

the propodeal triangle densely and deeply punctate, punctures separated by <0.5 puncture diameters (c.f. Fig. 65C) **4**

– Propodeum with clearly differentiated horizontal and vertical parts. Propodeum with or without punctures, but never with punctures separated by <0.5 puncture diameters **6**

4 Ocelloccipital distance 2.5–3 times the diameter of a lateral ocellus. Tergal discs occasionally red-marked .... ***variabilis*** **Smith**

– Ocelloccipital distance <2 times the diameter of a lateral ocellus. Tergal discs always dark **5**

5 S5 apically with extremely dense and pronounced latitudinal tuft of yellowish hairs. Terga with apical hair bands broadly interrupted. Typically flying earlier, May-June... ***labialis*** **(Kirby)**

– S5 apically without dense latitudinal hair tuft, at most with scattered hairs. Terga typically with clear and uninterrupted apical hair bands, though beware abraded specimens. Typically flying later, July-August......... ***decipiens*** **Schenck**

6 Discs of T2–3 entirely and conspicuously red-marked **7**

– Discs of T2–3 dark, at most with the apical margins lightened **8**

7 Large species, 11–13 mm. Mandibles long, sickle-like, crossing in their apical third (Fig. 74A). Head short, clearly broader than long. Genital capsule with gonostyli broad, weakly converging apically (Fig. 75G)....... ***schencki*** **Morawitz**

– Smaller species, never exceeding 9 mm. Mandibles normal, not strongly crossing apically. Head more or less round. Genital capsule with gonostyli apically narrow, strongly converging subapically (Fig. 75H) .... ***labiata*** **Fabricius**

8 Paraocular areas with markings narrow, running up the inner margin of the compound eye, clearly dorsally exceeding the antennal insertions (Fig. 75C). S8 with a ventrally projecting spine at each lateral margin .... ***orbitalis*** **Morawitz**

– Paraocular areas with markings more or less rectangular or quadrangular, never narrow and running up the inner margin of the compound eye (Fig. 75B); typically not exceeding the antennal insertions dorsally........... **9**

9 Fore margin of the clypeus clearly and strongly upturned. Pronotum with strong carinate humeral angle. Head broad, clearly broader than long........ **10**

– Fore margin of the clypeus normal, not upturned. Pronotum without a strong humeral angle. Head variable, but not strongly broadened........... **13**

10 Scutum strongly and densely punctate, punctures separated by 0.5–1 puncture diameter, underlying surface shagreened. A5 long, clearly exceeding the length of A4; A4 at most 0.6 times as long as A5. Larger, 9–10 mm .... ***griseobalteata*** **Dours**

– Scutum either strongly shagreened and obscurely punctate, or with shiny interspaces, never strongly punctured and shagreened. A5 short, not noticeably longer than A4, both segments quadrate or subquadrate. Smaller, 8–9 mm... **11**

11 Gena posteriorly rounded, without carina. All tarsi and the apex of the hind tibia lightened orange. Scutum strongly shagreened and obscurely punctate. Flying April-June .... ***chrysosceles* (Kirby)**

– Gena posteriorly with clear carina. Scutum with surface shiny between punctures **12**

12 Hind tarsi dark. Genital capsule with penis valves comparatively narrow. Associated with saline soils in southern Iberia. Flying March-June ....***juliana* Wood** (*partim*, with yellow markings on lower paraocular areas)

– Hind tarsi lightened orange. Genital capsule with penis valves broad, occupying the majority of the space between the gonostyli. Restricted to the Pyrenees. Flying July-August.. ***pallitarsis* Pérez**

13 Terga clearly and finely shagreened, dull to weakly shiny, with small and weak punctures. Facial markings yellow. Ocelloccipital distance short, equalling the diameter of a lateral ocellus. Restricted to central Spain.........***funerea* Warncke**

– Terga smooth and shiny between strongly pronounced punctures. Facial markings white. Ocelloccipital distance larger, at least 2 times the diameter of a lateral ocellus **14**

14 Larger, exceeding 10 mm in length. Mandibles basally with white markings. Body with abundant white pubescence, with dense hairs on the clypeus and ventrally on the gena that can obscure the underlying surface in fresh individuals. Widespread across all of Iberia. Flying April–July.............***leucolippa* Pérez**

– Small species, 7–8 mm. Mandibles dark, without basal white markings (Fig. 75B). Body with reduced pubescence, never with dense hairs that obscure the underlying surface. Rare, restricted to cool temperate habitats in and around the Pyrenees and Cantabrian Mountains. Flying July–August .. .. ***coitana* (Kirby)**

15 Discs of T2–3 clearly and extensively red-marked **16**

– Tergal discs dark, at most with the apical margins lightened **18**

16 Clypeus with yellow marking small, occupying only a small proportion of the clypeus medially, without internal black markings (Fig. 75F). Flying early in the year, March-May; widespread throughout Iberia. Associated with *Asphodelus* (Asphodelaceae)................................... ***sardoa* Lepeletier**

– Clypeus almost entirely pale, with two small black markings. Flying later in the year, from late May to August; restricted to temperate habitats across Spain, including mountains in eastern and south-eastern Spain Associated with scabious (former Dipsacaceae = Caprifoliaceae) **17**

17 Pronotum with strong humeral angle. Fore margin of the clypeus laterally produced into two small but distinctly projecting points (Fig. 76A). Smaller, 7–9 mm. Restricted to areas in and around the Pyrenees.........***marginata* Fabricius**

– Pronotum rounded. Fore margin of the clypeus normal, without lateral projections. Larger, 14–16 mm. Restricted to montane grasslands in northern and central Spain with isolated populations in the Sierra de Cazorla and Sierra Nevada......................... ***hattorfiana* (Fabricius)** (*partim*, light form)

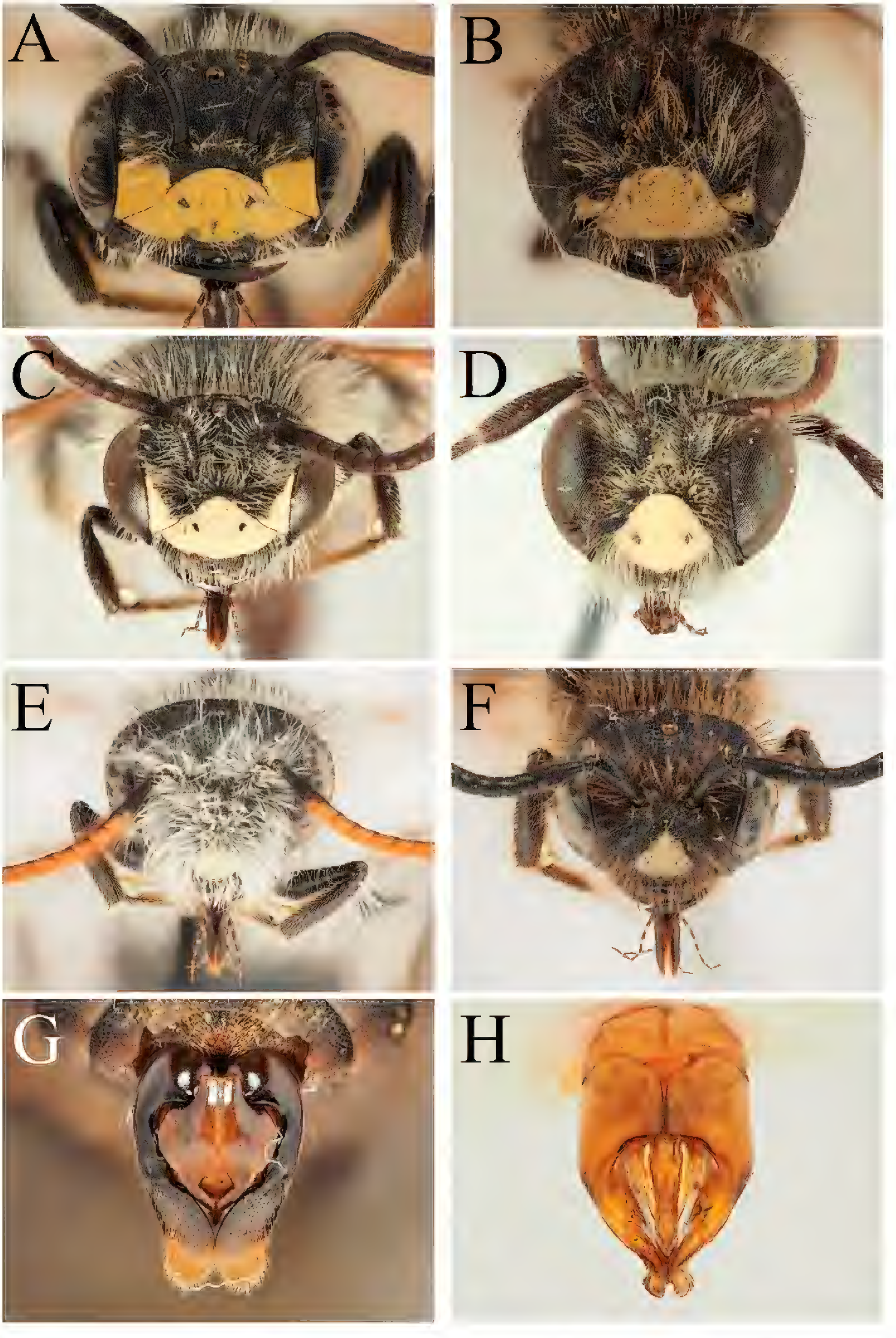

Figure 75. *Andrena* (*Opandrena*) *schencki* Morawitz, 1866, male **A** face, frontal view **G** genital capsule, dorsal view; *Andrena* (*Oreomelissa*) *coitana* (Kirby, 1802), male **B** face, frontal view; *Andrena* (*Rufandrena*) *orbitalis* Morawitz, 1871, male **C** face, frontal view; *Andrena* (*Orandrena*) *monilia* Warncke, 1975, male **D** face, frontal view; *Andrena* (*Truncandrena*) *doursana* Dufour, 1853, male **E** face, frontal view; *Andrena* (*Lepidandrena*) *sardoa* Lepeletier, 1841, male **F** face, frontal view; *Andrena* (*Poecilandrena*) *labiata* Fabricius, 1781, male **H** genital capsule, dorsal view.

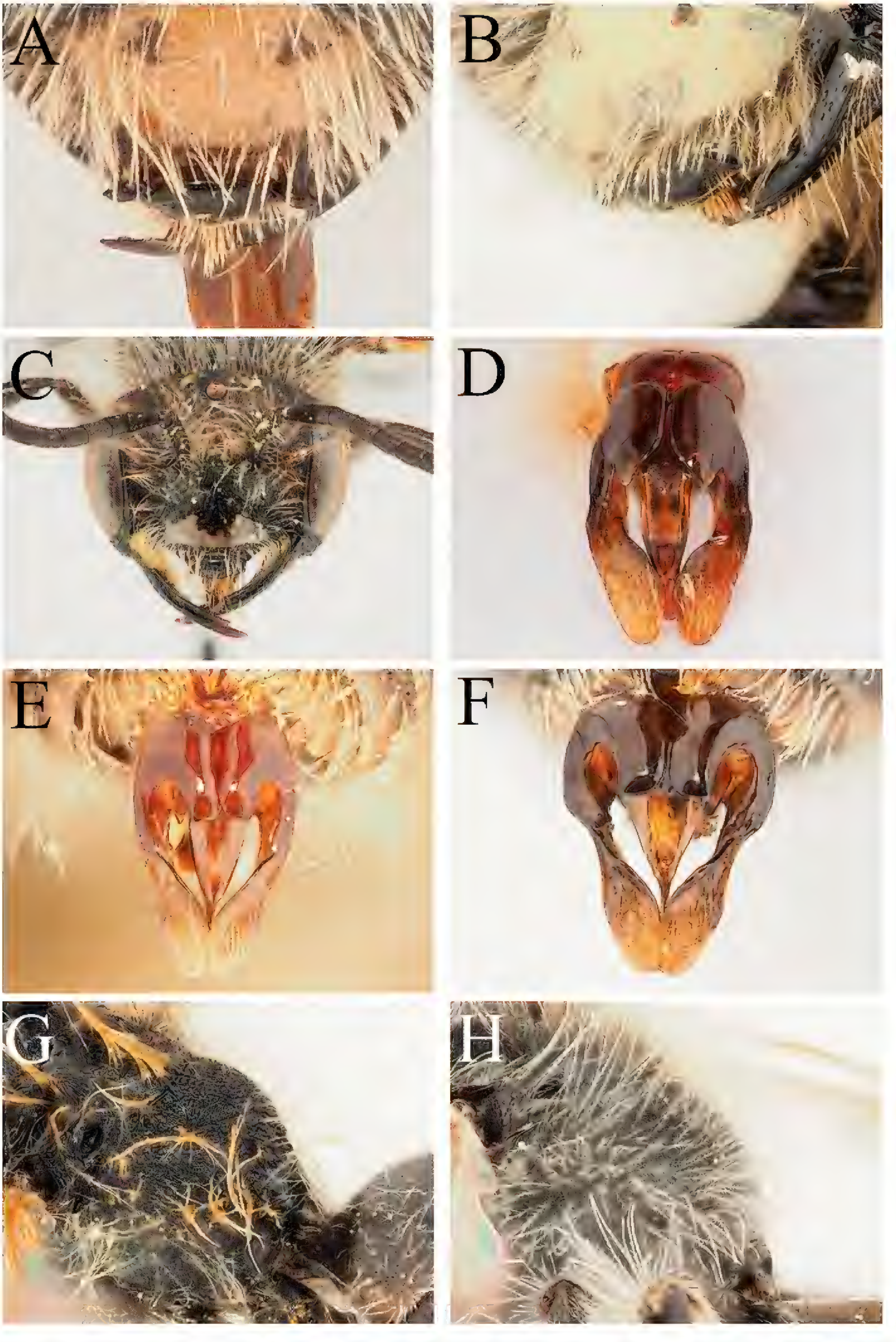

Figure 76. *Andrena* (*Margandrena*) *marginata* Fabricius, 1776, male **A** apex of clypeus, frontal view; *Andrena* (*Holandrena*) *flavilabris* Schenck, 1874, male **B** apex of clypeus, frontolateral view; *Andrena* (*Leucandrena*) *dinizi* Warncke, 1975, male **C** face, frontal view **F** genital capsule, dorsal view **G** propodeum, profile view; *Andrena* (*Leucandrena*) *tunetana* Schmiedeknecht, 1900, male **D** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *sericata* Imhoff, 1868, male **E** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *ventralis* Imhoff, 1832, male **H** propodeum, profile view.

18 Head, mesosoma, and/or metasoma with metallic green or blue reflections **19**
– Body lacking metallic reflections **24**
19 Yellow marking of clypeus very small, reduced to a narrow latitudinal strip at the fore margin of the clypeus (Fig. 75E) .... ***doursana* Dufour**
– Yellow or white marking of the clypeus always larger, covering the majority or the entirety of the clypeus (with exception of pair of small black dots) **20**
20 Discs of T2–4 clearly and densely punctate with strong punctures, punctures separated by ≤1 puncture diameter **21**
– Tergal discs with weaker and more scattered punctures, punctures either fine or separated by >1 puncture diameter **22**
21 Pronotum rounded. Tergal margins not strongly depressed, more or less at the same level as the tergal discs. Gena normal, as wide as the width of the compound eye. Restricted to high elevation sites in the Pyrenees .... ***viridescens* Viereck**
– Pronotum laterally carinate. Tergal margins strongly depressed, clearly lower than the level of the tergal discs. Gena broadened, clearly broader than the width of the compound eye. Found in central and southern Iberia.. ***bellidis* Pérez**
22 Larger, 8–10 mm. Scutum laterally shagreened, medially with a large more or less circular smooth and shiny area, this almost impunctate................... ....***aerinifrons* Dours**
– Smaller, 6–7 mm. Scutum uniformly shagreened and punctate, without a smooth and shiny area **23**
23 Inner hind tibial spurs strongly bent at their apexes. Body with subdued metallic reflections, almost without reflections................ ***varuga* Warncke**
– Inner hind tibial spurs straight, parallel-sided. Body with clear metallic reflections .... ***nigroviridula* Dours**
24 Fore margin of the clypeus upturned (Fig. 76B). Pronotum with a strong humeral angle **25**
– Fore margin of the clypeus normal, not upturned. Pronotum with or without a humeral angle **28**
25 Propodeum almost entirely declivous, without clearly differentiated horizontal and vertical parts. Propodeum with dorsolateral parts adjacent to the propodeal triangle densely and deeply punctate, punctures separated by <0.5 puncture diameters .... ***flavilabris* Schenck**
– Propodeum with clearly differentiated horizontal and vertical parts. Propodeum at most obscurely punctate..**26**
26 Larger, 10 mm. Scutum and scutellum shagreened, without shiny areas .... ***langadensis albipila* Warncke**
– Smaller, 6–7 mm. Scutum and scutellum at least medially with smooth and shiny areas **27**

27 Gena posteriorly carinate. Surface of gena predominantly smooth and shiny. Associated with saline soils in southern Iberia ....***juliana*** **Wood** (*partim*, with yellow markings restricted to the clypeus)

– Gena posteriorly rounded, without carina. Surface of gena microreticulate and dull. Very rate, recorded only from the Cádiz region, habitat preference unknown ....***microthorax*** **Pérez**

28 Mandibles elongate, sickle-like, strongly crossing in their apical third (Fig. 76C) AND pronotum with strong humeral angle AND gena broadened, clearly broader than the width of the compound eye, usually produced into a 90° angulation posteroventrally (yellow-faced *Leucandrena*) **29**

– Without this combination of characters; mandibles either shorter, pronotum laterally rounded, or gena not exceeding width of head **32**

29 Ocelloccipital distance short, <0.5 times the diameter of a lateral ocellus. Genital capsule with gonocoxal teeth apically strongly diverging, apexes pointed (Fig. 76D). Found in hot or Mediterranean areas in central and southern Iberia with Brassicaceae.................... ***tunetana*** **Schmiedeknecht**

– Ocelloccipital distance long, 1–2 times the diameter of a lateral ocellus. Genital capsule with gonocoxal teeth not strongly diverging, apexes truncate (Fig. 76E, F). Found in temperate areas in central and northern Iberia with *Salix* (Salicaceae)...**30**

30 Typically larger, 9–10 mm. Genital capsule more elongate, gonocoxal teeth with apexes comparatively narrow, gonostyli not noticeably constricted medially (Fig. 76E). Very rare, restricted to the Pyrenees ....***sericata*** **Imhoff**

– Typically smaller, 7–9 mm. Genital capsule more compact, gonocoxal teeth with apexes comparatively broad, gonostyli strongly constricted medially (Fig. 76F). More widespread across central and northern Iberia.............**31**

31 Lateral faces of the propodeum with a fine network of raised rugosity on top of the underlying granular microreticulation (Fig. 76G). Scutum with strong and obvious punctures, medially becoming smooth and shiny.. ***dinizi*** **Warncke**

– Lateral faces of the propodeum with regular granular microreticulation (Fig. 76H). Scutum obscurely punctate, uniformly microreticulate and dull..***ventralis*** **Imhoff**

32 Small species, length not exceeding 8 mm...**33**

– Larger species, at least 9 mm in length..**38**

33 Propodeal triangle with smooth granular microreticulation, without raised rugosity. Very small species, usually not exceeding 6 mm (yellow-faced *Aciandrena*)...**34**

– Propodeal triangle with at least some raised rugosity, never with uniformly smooth microreticulation. Usually a little larger, 6–8 mm.......................**35**

34 Terga regularly and clearly punctate, punctures extending onto depressed tergal margins. Throughout Iberia... ....***fulica*** **Warncke** (*partim*, light form with yellow clypeus)

– Terga obscurely punctate, punctures disappearing into underlying microreticulation, tergal margins more or less impunctate. Restricted to central and eastern Spain...***vacella*** **Warncke**

35 Hind basitarsi entirely lightened orange. Frons with contrasting black and white pubescence, black on the frons and gena posteriorly, intermixing with white around the antennal insertions, becoming white on the clypeus and on the gena ventrally. Restricted to *Potentilla*-rich (Rosaceae) cool habitats in the Pyrenees. Flying July-August................................ ***tarsata*** **Nylander**

– Hind basitarsi dark. Face with uniformly bright white or yellowish pubescence. Not restricted to the Pyrenees, usually flying earlier in the year **36**

36 Tergal discs covered with upstanding whitish pubescence, this forming dense apical hair bands on tergal margins in fresh individuals. Scutum anteriorly shagreened, becoming smooth and shiny posteriorly. Antennae ventrally strongly and extensively lightened orange. Restricted to south-western Spain (Huelva, Sevilla), flying March-April..***laurivora*** **Warncke**

– Tergal discs never with upstanding pubescence; white apical hair bands can be present on tergal margins. Scutum with uniform sculpture, consistently shiny across its surface. Antennae typically dark ventrally **37**

37 Disc of T1 with scattered punctures, punctures separated by 1–3 puncture diameters, strongly contrasting punctation of the discs of T2–4, here punctures separated by 0.5 puncture diameters. Clypeus yellow-marked across its entire surface with the exception of two small black marks. Genital capsule compact, with pronounced gonocoxal teeth and small and spatulate gonostyli (Fig. 77A). Restricted to central Spain .... ***taxana*** **Warncke**

– All tergal discs uniformly punctate, punctures separated by 0.5 puncture diameters. Clypeal marking often reduced in size, not covering entire surface. Genital capsule elongate, with weakly pronounced gonocoxal teeth, gonostyli apically produced into triangular wedges (Fig. 77B).................... .... ***ventricosa*** **Dours** (*partim*, light form)

38 Mid and hind basitarsi entirely lightened orange (Fig. 44B).....................**39**

– Mid and hind basitarsi dark...**41**

39 Ocelloccipital distance 3 times the diameter of a lateral ocellus. Terga very finely shagreened, more or less smooth and shiny. Tergal discs regularly and deeply punctate, punctures separated by 1–2 puncture diameters, punctures becoming smaller and continuing onto tergal margins. Genital capsule, see Fig. 44H.. ***limbata dusmeti*** **Warncke**

– Ocelloccipital distance <2 times the diameter of a lateral ocellus. Terga strongly shagreened, at most weakly shiny, tergal discs with small and obscure punctures that disappear into the underlying structure, tergal margins more or less impunctate...**40**

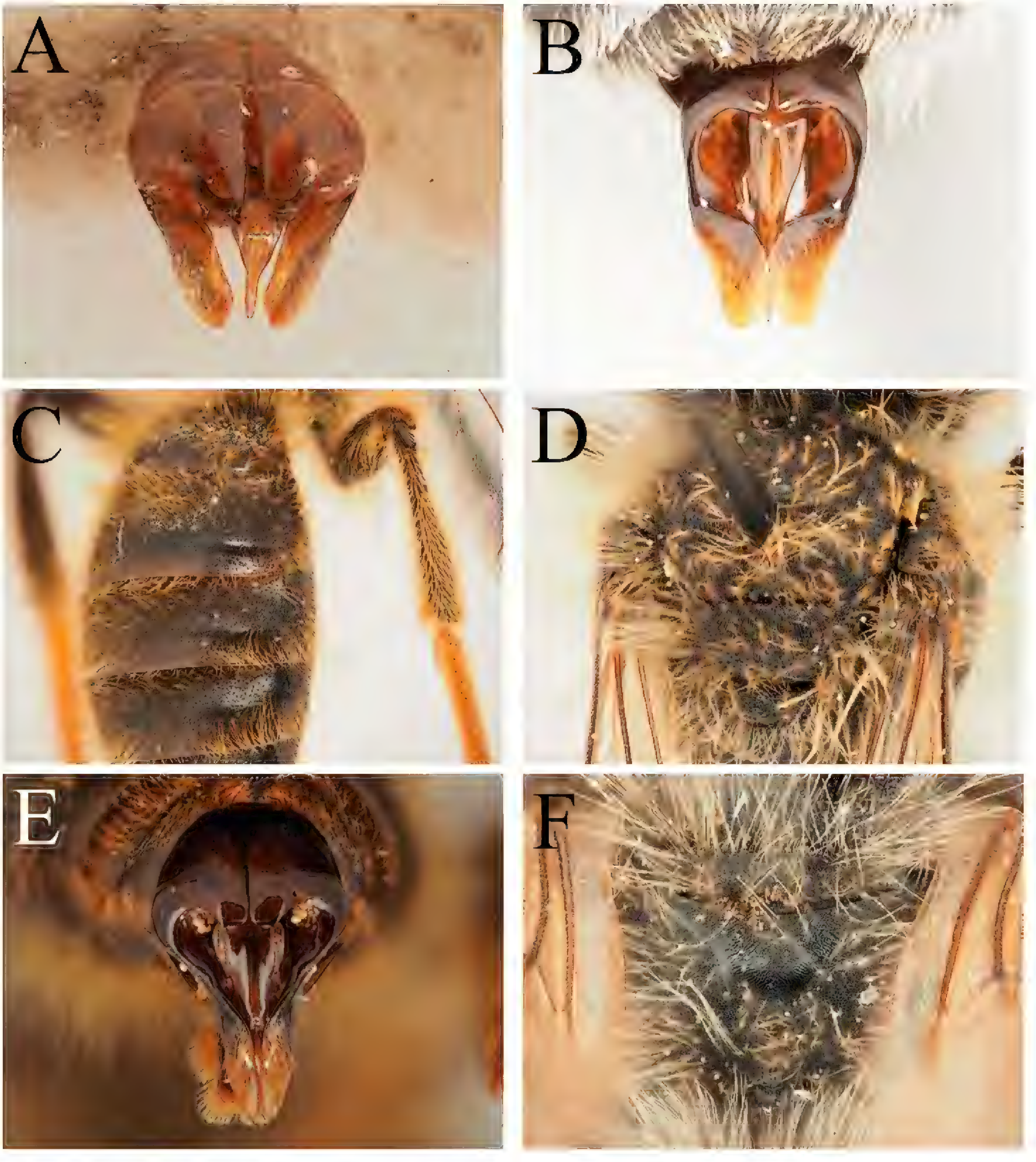

Figure 77. *Andrena* (*Parandrenella*) *taxana* Warncke, 1975, male **A** genital capsule, dorsal view; *Andrena* (*Cryptandrena*) *ventricosa* Dours, 1873, male **B** genital capsule, dorsal view; *Andrena* (*Truncandrena*) *minapalumboi* Gribodo, 1894, male **C** terga, dorsolateral view; *Andrena* (*Chlorandrena*) *rhyssonota* Pérez, 1895, male **D** scutum and scutellum, dorsal view; *Andrena* (*Charitandrena*) *hattorfiana* (Fabricius, 1775), male **E** genital capsule, dorsal view; *Andrena* (*Orandrena*) *monilia* Warncke, 1975, male **F** propodeum, dorsal view.

40 T2–5 laterally with extremely strong gradulus emerging from under the preceding terga, tergal margins of T1–4 elevated, not in contact with basal parts of T2–5 (Fig. 77C). Entire body with bright orange pubescence. Rare, known only from southern Spain (Alicante, Cádiz) .... ***minapalumboi* Gribodo**

– T2–5 laterally with very weak gradulus, margins of T1–4 not elevated, in contact with basal parts of T2–5. Body with paler pubescence, white hairs on face, gena ventrally, and mesepisternum, with light brown hairs dorsally. Common throughout Iberia .... ***ferrugineicrus* Dours**

41 Scutum and scutellum with dense network of raised longitudinal striations, most obvious on the scutellum (Fig. 77D). Tergal margins and tergal bases strongly depressed, giving individual tergal segments a domed appearance when viewed in profile .... ***rhyssonota* Pérez**

– Scutum and scutellum without longitudinal striations. Tergal margins depressed or not, but not in combination with tergal bases depressed **42**

42 Large species, 14–16 mm. Genital capsule distinctive, elongate with projecting and apically truncate gonocoxal teeth (Fig. 77E). Pubescence variable, from light brown to almost entirely black (ssp. *nigricauda* Wood). Restricted to montane grasslands in northern and central Spain with isolated populations in the Sierra de Cazorla and Sierra Nevada ....***hattorfiana* (Fabricius)** (*partim*, dark form)

– Smaller, sometimes reaching 14 mm, but usually 9–12 mm. Genital capsule different; if elongate, then gonocoxal teeth pointed, not truncate. Pubescence predominantly bright, never almost entirely black **43**

43 Face with strongly contrasting black and white pubescence; clypeus medially with white hairs, inner margins of the compound eyes and area around antennal insertions and frons with abundant black hairs **44**

– Face with bright pubescence, at most with occasional scattered dark hairs, never strongly contrasting light pubescence **46**

44 A3 short, only slightly longer than A4. A4 rectangular, only slightly longer than broad, clearly shorter than A5. Antennal segments slightly bulging ventrally. Rare, known only from southern Spain (Córdoba)............ ***varia* Pérez**

– A3 long, clearly longer than A4. A4 rectangular, clearly longer than broad, slightly shorter than A5. Antennal segments parallel-sided, without ventral bulges **45**

45 Genital capsule with apical flattened part elongate, longer than broad, appearing triangular (Fig. 51D, E). Inner margin of these flattened areas strongly and acutely raised, slightly reflexed. Larger, 13–14 mm. Known only from southern Spain (Málaga)................................***ghisbaini* sp. nov.**

– Genital capsule with apical flattened part rounded, as long as broad (Fig. 51F). Inner margin of these flattened areas less strongly raised and not reflexed. Smaller, 10–11 mm. Throughout Iberia .... ***villipes* Pérez**

46 Propodeal triangle broad, internal surface with very fine granular reticulation, laterally and posteriorly weakly shiny, contrasting the dorsolateral parts of the propodeum (Fig. 77F). Face in frontal view with compound eyes large, almost bulbous, separated by a distance only not greatly exceeding the diameter of an individual compound eye (Fig. 75D). Genital capsule elongate (Fig. 78A). Restricted to hot steppe in central Spain ....***monilia* Warncke**

– Propodeal triangle with clearer structure of raised reticulation or rugosity, without weakly shiny margins. Face in frontal view with compound eyes normal, separated by a distance much greater than the diameter of an individual compound eye (Fig. 78B). Genital capsule otherwise **47**

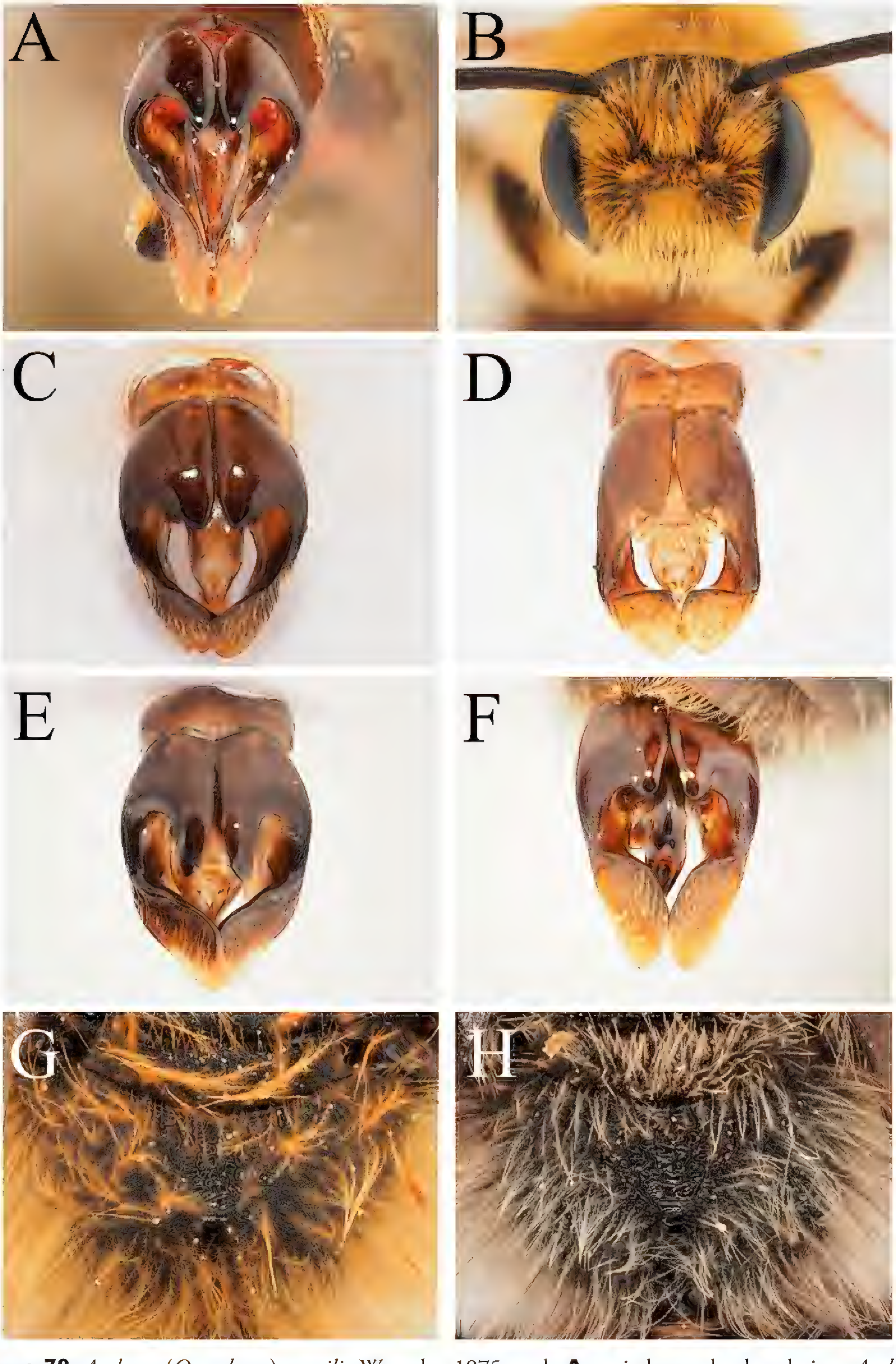

Figure 78. *Andrena* (*Orandrena*) *monilia* Warncke, 1975, male **A** genital capsule, dorsal view; *Andrena* (incertae sedis) *murana* Warncke, 1975, male **B** face, frontal view **D** genital capsule, dorsal view; *Andrena* (incertae sedis) *relata* Warncke, 1975, male **C** genital capsule, dorsal view; *Andrena* (*Chlorandrena*) *humilis* Imhoff, 1832, male **E** genital capsule, dorsal view; *Andrena* (*Truncandrena*) *nigropilosa* Warncke, 1967, male **F** genital capsule, dorsal view; *Andrena* (*Suandrena*) *suerinensis* Friese, 1884, male **G** propodeum, dorsal view; *Andrena* (*Plastandrena*) *pilipes* Fabricius, 1781, male **H** propodeum, dorsal view.

47 Terga finely shagreened, more or less smooth and shiny, regularly and deeply punctate, punctures separated by 1–2 puncture diameters, punctures extending onto the tergal margins. A3 comparatively short, only slightly exceeding length of A4. Nervulus antefurcal **48**

– Tergal shagreened to microreticulate, dull to weakly shiny, obscurely or clearly punctate, but marginal areas impunctate. A3 comparatively long, clearly exceeding length of A4. Nervulus interstitial to weakly postfurcal **49**

48 Genital capsule simple, with small gonocoxal teeth, gonostyli spatulate and more or less parallel-sided (Fig. 78C) .... ***relata* Warncke**

– Genital capsule complex, with inner margins progressively diverging, forming 90° inner angle. Gonostyli apically strongly flattened and broadened, more or less triangular shovel-like (Fig. 78D) .... ***murana* Warncke**

49 Disc of T1 with large 'crater punctures', punctures with distinctly raised margins. Terga shagreened and weakly shiny. Genital capsule with long, strongly produced gonocoxal teeth (Fig. 78E) .... ***humilis* Imhoff**

– Disc of T1 with small hair-bearing punctures, without raised, crater-like rims. Terga microreticulate and dull. Genital capsule with only weakly produced gonocoxal teeth **50**

50 A3 very long, slightly exceeding the length of A4+5. A4 very short, broader than long. Genital capsule relatively compact, with flattened apical part clearly longer than broad .... ***medeninensis donata* Warncke**

– A3 comparatively shorter, at most equalling the length of A4+5. A4 longer, slightly longer than broad. Genital capsule relatively elongate, with flattened apical part only slightly longer than broad (Fig. 78F) .... ***nigropilosa* Warncke**

51 (1) Propodeal triangle clearly defined by strongly raised carinae, internal surface rugose-areolate (Figs 78G, H, 79A) **52**

– Propodeal triangle not strongly defined by lateral carinae with its internal surface rugose-areolate **66**

52 Forewing with two submarginal cells. Clypeus with longitudinal striations. .... ***lagopus* Latreille**

– Forewing with three submarginal cells. Clypeus without longitudinal striations **53**

53 Small species, 6–7 mm. Clypeus, scutum, and terga extremely densely and deeply punctate with small punctures, punctures almost confluent. Each side of T2 laterally with a small but deep and clearly defined fovea (Fig. 79B, C; subgenus *Brachyandrena*) **54**

– Larger species, at least 8 mm in length, usually >10 mm. Body never so densely punctate, punctures always a little separated, never confluent. T2 with fovea obscure **55**

54 T2 laterally with foveae narrow and relatively elongate (Fig. 79B). Common and widespread across Iberia[18]................................ ***colletiformis* Morawitz**

– T2 laterally with foveae shorter and relatively broad (Fig. 79C). Rare, encountered predominantly in southern Spain (Cádiz, Málaga)[18]....... ***miegiella* Dours**

55 Pronotum laterally with strong humeral angle with well-developed carina. Fore margin of clypeus weakly upturned.......................... ***fuscosa* Erichson**

– Pronotum laterally rounded. Fore margin of clypeus normal, not upturned **56**

56 Hind basitarsi and majority of hind tibiae lightened orange. Body with integument uniformly dark. Pubescence bright, face and mesepisternum with light brown hairs, scutum and T6 with bright orange hairs. A3 clearly shorter than A4.. ***haemorrhoa* (Fabricius)**

– Without this combination of characters; either hind legs dark, body with darker pubescence, or A3 clearly longer than A4.................................... **57**

57 Terga with metallic reflections and at most superficial punctures AND genital capsule distinctive, with strongly produced gonocoxal teeth and gonostyli strongly reflexed, with long plumose hairs present on their outer margin (subgenus *Suandrena*) **58**

– Terga without metallic reflections OR if with metallic reflections, then genital capsule otherwise, either lacking pronounced gonocoxal teeth or without plumose hairs on the outer margin of the gonostyli OR terga clearly and abundantly punctate (subgenus *Plastandrena*) **60**

58 Genital capsule with penis valves grossly inflated, occupying entirety of space between the gonostyli, laterally produced into bulbous projections (Fig. 79D). Known only from Cádiz province, flying in December............ .... ***gades* Wood & Ortiz-Sánchez**

– Genital capsule with penis valves narrower, essentially parallel-sided, not occupying entirety of space between the gonostyli, without lateral projections... **59**

59 A3 ventrally rounded, lacking any kind of triangular point (Fig. 79E). Genital capsule less elongate, gonocoxal teeth relatively short (Fig. 79F). Confirmed males known only from eastern and southern Spain. Bivoltine, flying February-April and September-October........................ ***cyanomicans* Pérez**

– A3 ventrally produced into triangular point (Fig. 79G). Genital capsule more elongate, with long and strongly produced gonocoxal teeth (Fig. 79H). Widespread across Iberia. Univoltine, flying March-May....... .... ***suerinensis* Friese**

60 Genital capsule with gonocoxae apically rounded (Fig. 80A, B).............. **61**

– Genital capsule with clearly produced gonocoxal teeth (Fig. 80C–G)........ **62**

18 These two species are very difficult to separate in the male sex. Association with females should be made, as well as taking account of their known distributions.

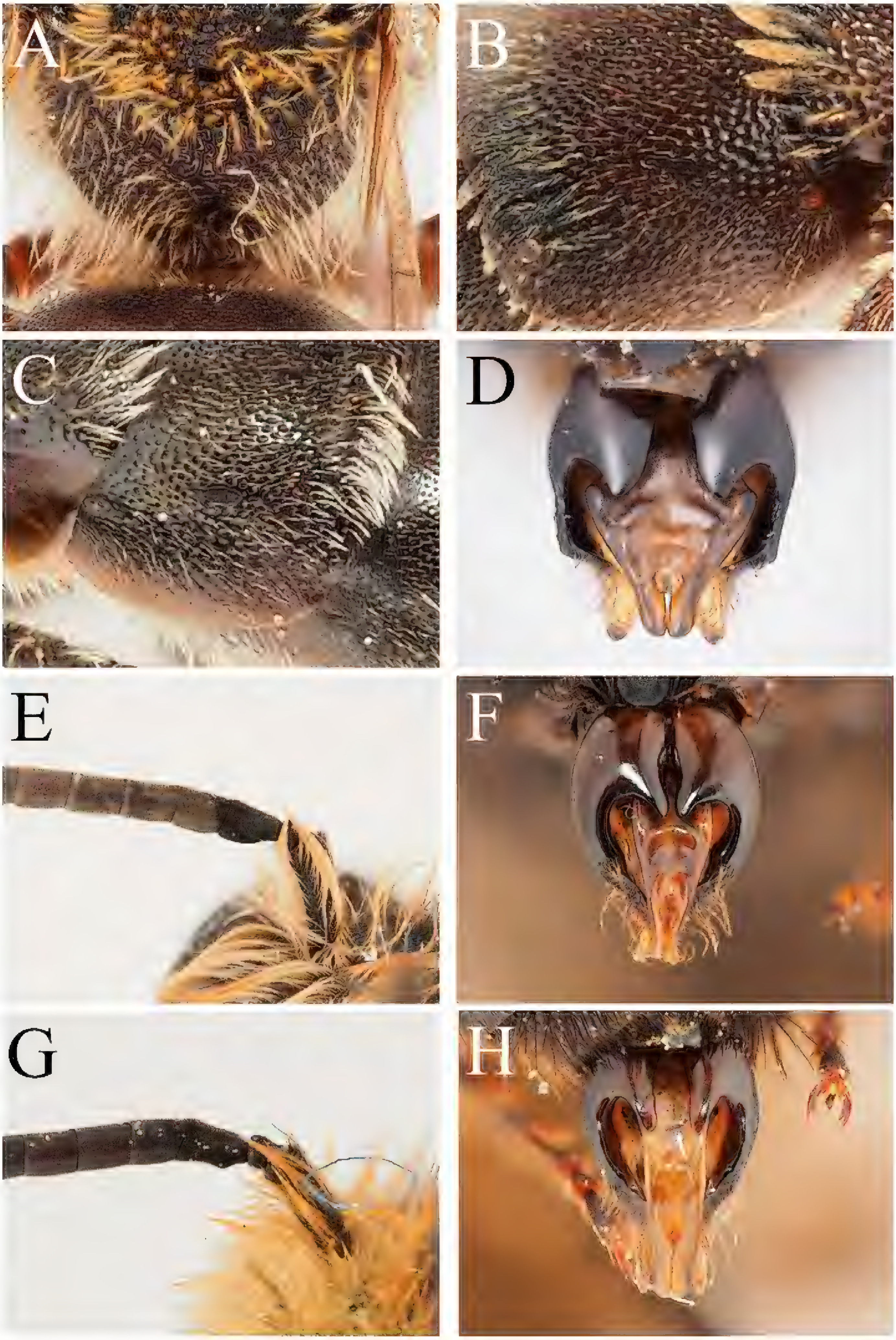

Figure 79. *Andrena* (*Brachyandrena*) *colletiformis* Morawitz, 1873, male **A** propodeum, dorsal view **B** T2, profile view; *Andrena* (*Brachyandrena*) *miegiella* Dours, 1873, male **C** T2, profile view; *Andrena* (*Suandrena*) *gades* Wood & Ortiz-Sánchez, 2022, male **D** genital capsule, dorsal view; *Andrena* (*Suandrena*) *cyanomicans* Pérez, 1895, male **E** antennae, frontal view **F** genital capsule, dorsal view; *Andrena* (*Suandrena*) *suerinensis* Friese, 1884, male **G** antennae, frontal view **H** genital capsule, dorsal view.

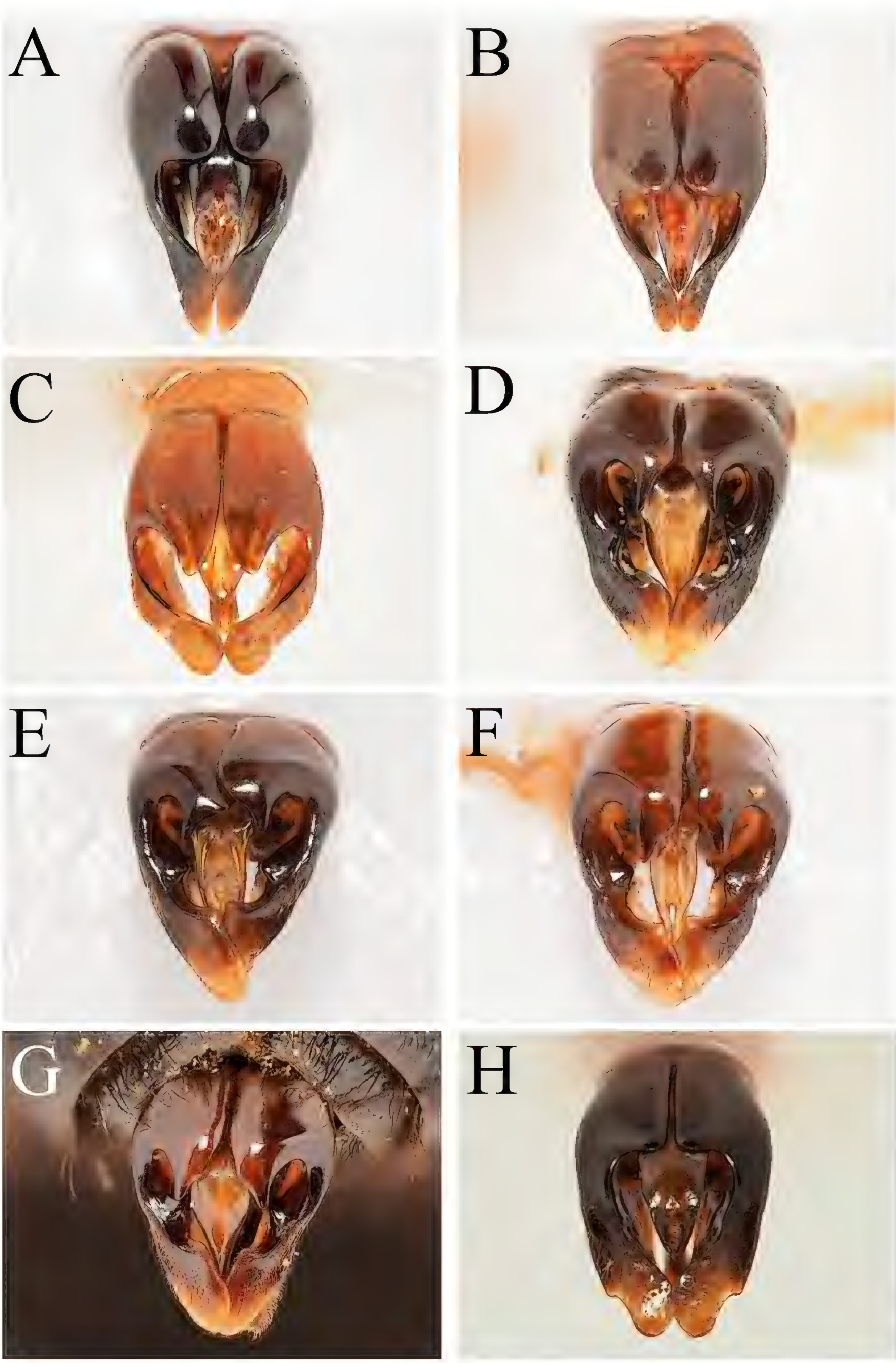

Figure 80. *Andrena* (*Plastandrena*) *agilissima* (Scopoli, 1770), male **A** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *afrensis* Warncke, 1967, male **B** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *asperrima* Pérez, 1895, male **C** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *tibialis* (Kirby, 1802), male **D** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *bimaculata* (Kirby, 1802), male **E** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *pilipes* Fabricius, 1781, male **F** genital capsule, dorsal view; *Andrena* (*Plastandrena*) *nigrospina* Thomson, 1872, male **G** genital capsule, dorsal view; *Andrena* (*Melandrena*) *flavipes* Panzer, 1799, male **H** genital capsule, dorsal view.

61 Terga with metallic blue reflections. Genital capsule with penis valves medially with and oval hyaline expansion, this breaking the profile of the penis valves themselves (Fig. 80A). Gonostyli with inner margin raised .... ***agilissima* (Scopoli)**

– Terga dark, without metallic blue reflections. Genital capsule penis valves uniformly converging apically (Fig. 80B). Gonostyli with inner margin not raised .... ***afrensis* Warncke**

62 Terga usually extremely densely punctate, punctures almost confluent. Terga with weak metallic blue hints. Genital capsule, see Fig. 80C, see also Fig. 25D .... ***asperrima* Pérez**

– Terga never so densely punctate, punctures never confluent, always separated by at least 0.5 puncture diameters. Terga never with metallic blue reflections. Genital capsule otherwise..**63**

63 Mesosoma with brown pubescence dorsally and laterally, at most with occasional black hairs **64**

– Mesosoma with grey and black pubescence, always with at least some black hairs laterally on the mesepisternum **65**

64 Genital capsule with penis valves basally broad (Fig. 80D). Nominally univoltine, flying only in the spring .... ***tibialis* (Kirby)**

– Genital capsule with penis valves basally narrow (Fig. 80E). Bivoltine, flying in the spring and the summer .... ***bimaculata* (Kirby)**

65 Penis valves basally narrow, apical spatulate parts of gonostyli comparatively narrow (Fig. 80F). Bivoltine (typically March–April and July–August). Common and widely distributed throughout Iberia......... ***pilipes* Fabricius**

– Penis valves basally broad, apical spatulate parts of gonostyli comparatively broad (Fig. 80G). Univoltine (typically May–June). Rare, restricted to mountainous parts of Iberia; known from the Pyrenees, the Sistema Central, Serra do Gerês, Sistema Ibérico, and Sierra de Cazorla........................ .... ***nigrospina* Thomson**

66 (51) Genital capsule distinctive, with more or less 90° emargination in the outer parts of the gonostyli (Fig. 80H). The most common *Andrena* species in Iberia .... ***flavipes* Panzer**

– Genital capsule otherwise **67**

67 Process of the labrum thickened and expanded, anteriorly projecting beyond the fore margin of the clypeus. Pronotum with strong humeral angle. Active in the summer (mid-June to September) (subgenus *Cnemidandrena* and remaining *Margandrena*) **68**

– Without this combination of characters...**71**

68 T2–3 extensively red-marked. Clypeus with apical corners produced into distinct anteriorly projecting knobs (c.f. Fig. 76A). Restricted to north-eastern Spain in Mediterranean habitats .... ***pellucens* Pérez**

– Terga dark, without red markings. Clypeus without apically projecting knobs...**69**

69 Outer surface of the galea smooth and shiny. Associated with Ericaceae, found in Atlantic habitats across northern, central, and western Iberia........ .... ***fuscipes* (Kirby)**

– Outer surface of the galea shagreened and dull.......................................**70**

70 Gena posteriorly produced into a strong winged carina. Scutum with abundant black hairs. Associated with Asteraceae, restricted to northern Spain... .... ***denticulata* (Kirby)**

– Gena posteriorly rounded. Scutum at most with occasional black hairs, usually entirely brown-haired. Polylectic, though often found on Asteraceae. Restricted to areas surrounding the Pyrenees with isolated populations in high mountains in southern Spain (particularly the Sierra Nevada)............ .... ***nigriceps* (Kirby, 1802)**

71 (67) Fore margin of clypeus upturned AND gena conspicuously broadened, wider than the width of the compound eye AND pronotum with a conspicuous humeral angle (remaining *Notandrena*) **72**

– Without this exact combination of characters. (Note, male members of the *Ovandrena* are very similar, but the gena is as broad as the width of the compound eye, not broader. They can be found at couplet 168; *Andrena blanda* is also similar, but the gena is only slightly wider than the width of the compound eye. It should be diagnosed by its genital capsule, go to couplet 184)..**76**

72 Mandibles long, sickle-shaped, strongly crossing apically. A3 long, exceeding length of A4+5. Clypeus covered with dense plumose hairs than obscure the underlying surface in fresh specimens. Clypeus sometimes with weak metallic reflections **73**

– Mandibles normal, not sickle-shaped, not strongly crossing apically. A3 short, slightly shorter than A4+5. Clypeus without plumose hairs that obscure the underlying surface. Clypeus dark, without metallic reflections **75**

73 Terga uniformly dark, at most with marginal areas lightened dark brown. A3 comparatively short, only moderately exceeding length of A4+5. Discs of T2–4 clearly and regularly punctate, punctures separated by 2 puncture diameters, underlying surface shagreened and weakly shiny .... ***ranunculi* Schmiedeknecht**

– Terga red-marked, with at least marginal areas and lateral parts of T2–3 lightened red. A3 comparatively long, almost equalling or equalling length of A4+5+6. Terga shagreened, obscurely punctate, punctures disappearing into background sculpture **74**

74 Clypeus polished and shiny, with scattered punctures. Mesonotum with shiny areas medially. A3 equalling A4+5+6 .... ***binominata* Smith**

– Clypeus uniformly shagreened and dull. Scutum uniformly shagreened and dull. A3 slightly shorter than A4+5+6...................... ***leucophaea* Lepeletier**

75 Terga with marginal areas of T2–4 puncture-free. A3 shorter than A4+5, never twice as long as A4. Basitarsi usually dark, sometimes apically lightened

orange. Restricted to cooler parts of northern and western Iberia; univoltine, flying on July-August .... ***nitidiuscula* Schenck**

– Terga with punctures of discs of T2–4 extending onto marginal areas. A3 almost as long as A4+5, typically twice as long as A4. Basitarsi usually entirely lightened orange. Widespread across Iberia; bivoltine, flying in April-May and July-August .... ***fulvicornis* Schenck**

76 (71) Small species, body length of 5–7 mm, terga always dark, legs always dark (remaining *Aciandrena*, *Aenandrena partim*, *Avandrena*, *Cordandrena partim*, *Cryptandrena partim*, *Graecandrena*, and almost all *Micrandrena*) **77**

– Larger species, at least 8 mm in length. Terga lightened red in some species, either on the discs or the margins. Hind tarsi or basitarsi lightened orange in some species **121**

77 All tergal discs uniformly punctate, punctures separated by 0.5 puncture diameters, underlying surface weakly shiny. Genital capsule elongate, with weakly pronounced gonocoxal teeth, gonostyli apically produced into triangular wedges (Fig. 77B) .... ***ventricosa* Dours** (*partim*, dark form)

– Genital capsule otherwise; tergal punctation variable **78**

78 A3 much shorter than A4, at most ½ the length (Fig. 81A, C). Terga often with weak metallic bronzy reflections (Fig. 81D) **79**

– A3 as long as A4 or longer. Terga without metallic reflections **81**

79 A3 extremely short relative to A4, at most $^1/_5$ the length (Fig. 81A). Terga dark. Genital capsule distinctive, with extremely narrow parallel-sided penis valves (Fig. 81B). Rare, known from eastern Spain (Jáen, Soria, Teruel).................................. ***vaulogeri* Pérez** (*partim*, small individuals)

– A3 not so short, around ½ the length of A4 (Fig. 81C). Terga with metallic bronzy reflections. Genital capsule otherwise **80**

80 T3–4 laterally almost impunctate, any obscure punctures disappear into the background sculpture .... ***aeneiventris* Morawitz**

– T3–4 laterally with abundant clear punctures, these distinct against the background structure (Fig. 81D) .... ***hedikae* Jäger**

81 A3 long, equalling or exceeding length of A4+5. Face with abundant dark pubescence, sometimes intermixed with white hairs. Propodeal triangle narrow, with fine granular shagreenation over the majority of its area, sometimes with short, fine, and raised rugae basally (Fig. 82A). Scutum shagreened, dull to weakly shiny, with obscure scattered punctures. Metasoma with obscure and scattered hair-bearing punctures, punctures separated by 3–4 puncture diameters. Active in the early spring (March-April), associated with *Erodium* (Geraniaceae; subgenus *Avandrena*) **82**

– Without this combination of characters.. **84**

82 Genital capsule relatively compact, gonostyli apically flattened, more or less triangular shovel-like, more or less as broad as long (Fig. 82B). Tergal discs

Figure 81. *Andrena* (*Cordandrena*) *vaulogeri* Pérez, 1895, male **A** antennae, frontal view **B** genital capsule, dorsal view; *Andrena* (*Aenandrena*) *hedikae* Jäger, 1934, male **C** antennae, frontal view **D** terga, posterolateral view.

very finely shagreened, almost smooth and shiny. Known from southern Spain (Albacete, Cádiz, Granada, Málaga) .... ***melacana* Warncke**

– Genital capsule elongate, gonostyli with apical flattened part much longer than broad (Fig. 82C, D). Tergal discs more strongly shagreened, at most weakly shiny **83**

83 Viewed ventrally, process of S8 narrow, more or less the same width as the basal stem part (Fig. 82E). Smaller, 6–7 mm[19] ....***panurgina* De Steffani**

– Viewed ventrally, process of S8 large, clearly broader than the basal stem part (Fig. 82F). Slightly larger, 7–8 mm[19].. ...... ***avara* Warncke aggregate** (potentially including multiple valid species)

19 Because of taxonomic complexity and variation in the shape of the genital capsule within *A. avara* (e.g. the capsule pictured here in Fig. 82D is *A. avara liturata* Warncke, 1975 that has apically truncate gonocoxal teeth), it is best to use only the form of S8 to separate *A. panurgina* from the *A. avara* complex.

Figure 82. *Andrena* (*Avandrena*) *panurgina* De Steffani, 1889, male **A** propodeal triangle **C** genital capsule, dorsal view **E** S8, ventral view; *Andrena* (*Avandrena*) *melacana* Warncke, 1967, male **B** genital capsule, dorsal view; *Andrena* (*Avandrena*) *avara liturata* Warncke, 1975, male **D** genital capsule, dorsal view **F** S8, ventral view.

84 Propodeal triangle smooth, not defined laterally by raised carinae, with internal surface lacking network of raised rugosity, at most with very short rugae at the base of the propodeal triangle (Fig. 52D) **85**

– Propodeal triangle either strongly defined by raised carinae, or with internal surface with network of raised rugosity covering at least the basal half (specifically, take care with *A. tenuistriata*, for which the lateral parts of the propodeal triangle present granular shagreen) **95**

85 Clypeus with clear longitudinal striations covering the entire surface. Restricted to sandy and usually coastal habitats in southern Iberia........... ***orana*** **Warncke**

– Clypeus without striations, or with at most obscure striations at the base of the clypeus, never covering the entire surface **86**

86 Clypeus weakly but distinctly domed, basally densely punctate, punctures separated by 0.5 puncture diameters, punctures becoming sparse apically, here separated by 2–3 puncture diameters; underlying surface smooth and shiny (Fig. 83A). Fore margin of the clypeus forming a very wide and gentle emargination, process of the labrum narrow, slightly longer than wide. Genital capsule, see Fig. 83B............................ ***pandosa trigona*** **Warncke**

– Without this combination of characters, clypeus usually flattened and/or shagreened and dull, or genital capsule otherwise.................................... **87**

87 Terga strongly and clearly punctate, tergal margins strongly depressed, with punctures continuing onto marginal areas; underlying surface finely shagreened and weakly shiny. Very small species, not exceeding 6 mm............. ....***fulica*** **Warncke** (*partim*, dark form with black clypeus)

– Terga either impunctate (Fig. 52E) or obscurely punctate, without clear punctures extending onto the tergal margins... **88**

88 Clypeus flattened, shagreened in basal half, finely shagreened in apical half, the two half therefore contrasting; surface with obscure and scattered punctures. Genital capsule elongate, with long and sharply pointed penis valves (Fig. 83C)... ***verticalis*** **Pérez**

– Clypeus flattened or domed, but without this combination of characters. Genital capsule otherwise **89**

89 Genital capsule unusual, gonocoxae with inner margins forming obtuse angle, without gonocoxal teeth, gonostyli flattened with square truncate apexes (Fig. 83D, E) **90**

– Genital capsule otherwise **91**

90 Genital capsule with gonostyli comparatively narrow, apically narrower than the basal width of the penis valves; penis valves occupying comparatively little of the space between the gonostyli (Fig. 83D). Restricted to the extreme north-east of Spain... ***impunctata*** **Pérez**

– Genital capsule with gonostyli comparatively broad, apically as broad as the basal width of the penis valves; penis valves occupying majority of space between the gonostyli (Fig. 83E). Restricted to central, southern, and eastern Spain, not known from the north-east .... ***nebularia*** **Warncke**

91 Tergal margins extensively lightened hyaline-yellow, T2–4 with dense and thick complete apical hair bands that occupy and slightly exceed the entire length of the margin, obscuring the underlying surface in fresh individuals. Small species, not exceeding 6 mm. Rare, known only from central Spain .... ***montarca*** **Warncke**

– Tergal margins with weaker apical hair bands, tergal margins not so extensively lightened yellow. If in doubt, species exceeding 6 mm in length, or with clypeus flattened **92**

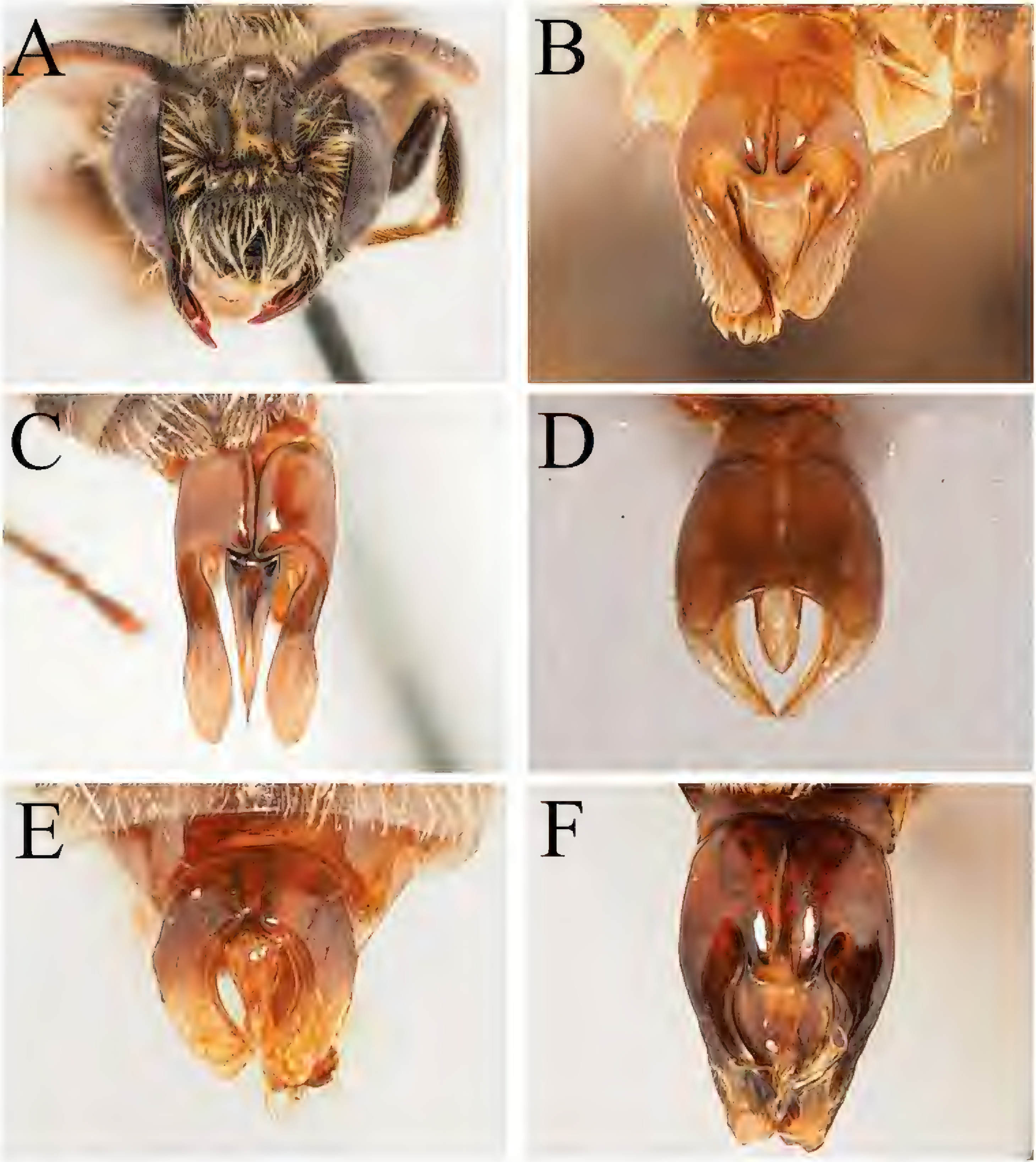

Figure 83. *Andrena* (*Micrandrena*) *pandosa trigona* Warncke, 1975, male **A** face, frontal view **B** genital capsule, dorsal view; *Andrena* (*Graecandrena*) *verticalis* Pérez, 1895, male **C** genital capsule, dorsal view; *Andrena* (*Graecandrena*) *impunctata* Pérez, 1895, male **D** genital capsule, dorsal view; *Andrena* (*Graecandrena*) *nebularia* Warncke, 1975, male **E** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *longibarbis* Pérez, 1895, male **F** genital capsule, dorsal view.

92 Genital capsule with penis valves basally strongly swollen, blister-like, gonocoxae with well-developed gonocoxal teeth (Fig. 83F)............................**93**

– Genital capsule with penis valves normal, not noticeably broadened (Fig. 52F)..**94**

93 A3 shorter than A4+5. Clypeus flattened, with slight metallic green-purple hints medially. Terga essentially impunctate. Widespread across Iberia .... ***longibarbis* Pérez**

– A3 slightly longer than A4+5. Clypeus flattened, almost with slight longitudinal concavity medially, uniformly black. Terga obscurely punctate. Central and eastern Spain only.. ***fria* Warncke**

94 Gena broad, clearly broader than the width of a compound eye (Fig. 52B, C). Scutum with obscure and shallow but large, hair-bearing punctures, punctures separated by 2–3 puncture diameters. Pronotum with strong humeral angle. Widespread across western and southern Iberia........................ ***alma* Warncke**

– Gena normal, equalling the width of a compound eye. Scutum extremely obscurely punctate, punctures disappearing into background structure. Pronotum rounded. Presence and distribution in Iberia unclear........... ***abjecta* Pérez**

95 Genital capsule distinctive, with strongly reflexed gonostyli (Fig. 84A) .... ***djelfensis* Pérez**

– Genital capsule otherwise **96**

96 Genital capsule with penis valves clearly and strongly broadened basally, clearly bulbous in appearance (Fig. 84B–D).. **97**

– Genital capsule with penis valves not strongly broadened basally **100**

97 Marginal area of T1 wide, strongly thickened, impunctate. Scutum with scattered punctures, punctures separated by 1–3 puncture diameters. Genital capsule with gonocoxal teeth weakly produced (Fig. 84B) Restricted to mountainous areas in northern Spain, associated with *Potentilla* (Rosaceae) .... ***falsifica* Perkins**

– Marginal area of T1 not strongly thickened, flat or slightly depressed. Genital capsule with gonocoxal teeth truncate (Fig. 84C, D). Scutum densely punctate, punctures separated by 0.5–1 puncture diameter..................... **98**

98 Clypeus flattened, with slight longitudinal impression medially. Inner margin of the gonostyli upturned, diverging dorsally from outer margin, forming a slight but visible 'kink' (Fig. 84C). Associated with *Ornithogalum* (Asparagaceae) .... ***saxonica* Stöckhert**

– Clypeus less strongly flattened. Inner margin of the gonostyli parallel with the outer margin, without a visible 'kink' (Fig. 84D). Associated with a wider variety of flowering plants **99**

99 Restricted to areas close to the Pyrenees. A4 slightly longer than A6. Broadened penis valves comparatively longer[20] .... ***strohmella* Stöckhert**

– Found in mountainous areas across southern and central Spain and northern Portugal. A4 as long as A6. Broadened penis valves comparatively shorter[20] .... ***icterina* Warncke**

20 These two species are very difficult to separate morphologically; geographic context should be used.

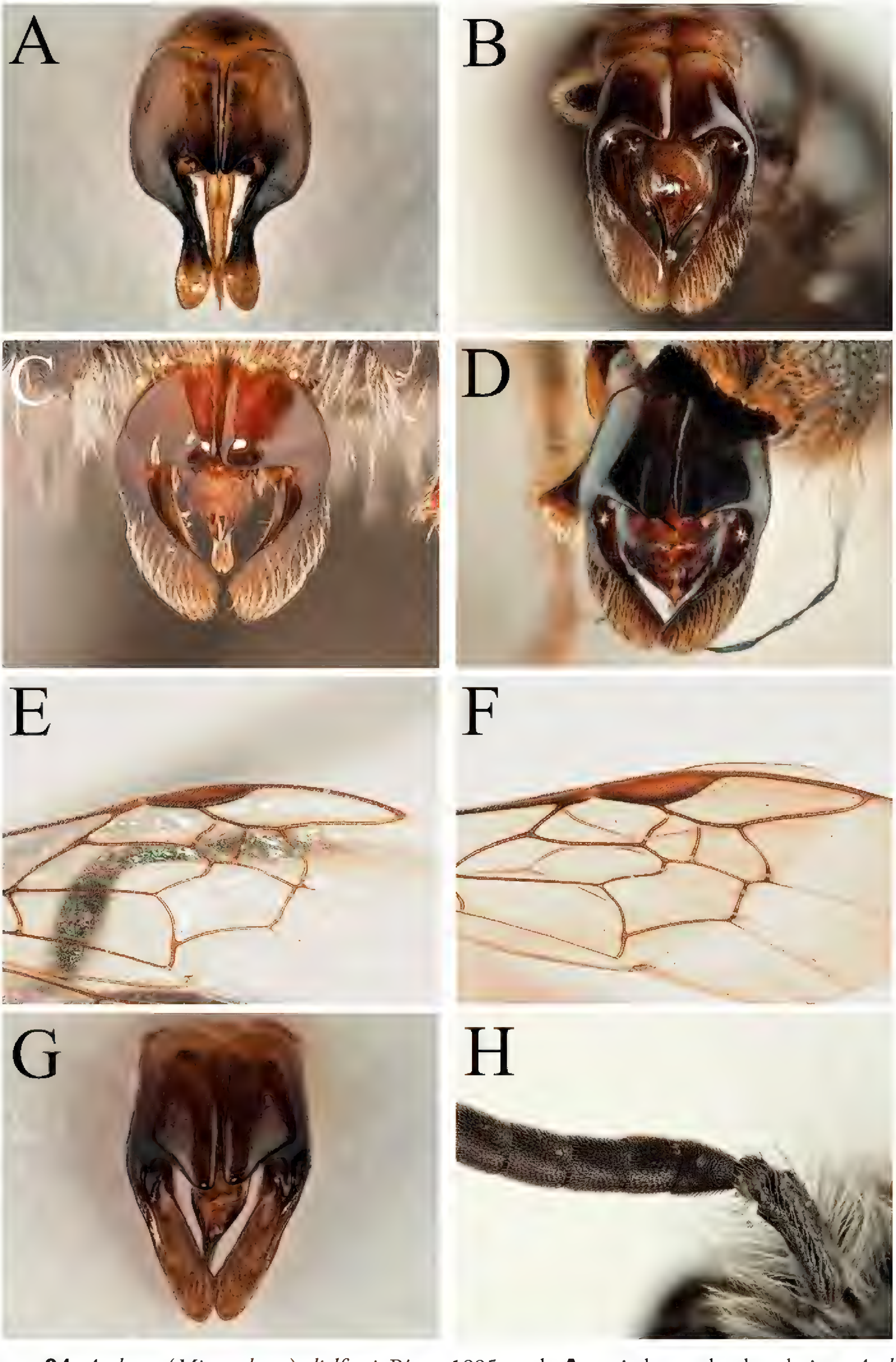

Figure 84. *Andrena* (*Micrandrena*) *djelfensis* Pérez, 1895, male **A** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *falsifica* Perkins, 1915, male **B** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *saxonica* Stöckhert, 1935, male **C** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *icterina* Warncke, 1974, male **D** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *nana* (Kirby, 1802), male **E** forewing, dorsal view **F** *Andrena* (*Micrandrena*) *fabrella* Pérez, 1903, male **F** forewing, dorsal view **G** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *semilaevis* Pérez, 1903, male **H** antennae, frontal view.

100 Genital capsule with outer margins of the gonostyli concave. Clypeus strongly shagreened and dull.......................... ***simontornyella*** **Noskiewicz**

– Genital capsule with outer margins of the gonostyli essentially parallel with the inner margin...**101**

101 Clypeus flattened, basally with obscure but distinct longitudinal striations, these covering the basal quarter of the clypeus and are channelled laterally along its margins...**102**

– Clypeus typically domed, without longitudinal striations basally..........**103**

102 Facial pubescence predominantly black. Scutum shagreened with faint and weak greasy metallic reflections. Tergal discs shagreened, weakly shiny. Tergal margins distinctly depressed. Widespread throughout Iberia..... ***nitidula*** **Pérez**

– Facial pubescence predominantly pale, with scattered black hairs laterally. Scutum more strongly shagreened, matt. Tergal discs with strong microreticulation, dull. Tergal margins weakly depressed. Restricted to the extreme north-east of Spain... ***distinguenda*** **Schenck**

103 Genital capsule elongate with penis valves converging apically to form a tapering point (Fig. 20A, B). Propodeum with propodeal triangle broad, laterally poorly defined with lateral carinae becoming shorter and weaker posteriorly...**104**

– Genital capsule and propodeal triangle otherwise.................................**105**

104 Genital capsule with the inner margins of the gonostyli only weakly produced towards the penis valves; apical spatulate part of the gonostyli comparatively elongate (Fig. 20A). Tergal discs typically more shagreened and dull, punctures disappearing somewhat into underlying sculpture .... ***niveata*** **Friese**

– Genital capsule with the inner margins of the gonostyli strongly produced towards the penis valves; apical spatulate part of the gonostyli comparatively short (Fig. 20B). Tergal discs typically smooth and shiny, punctures clearly visible .... ***lecana*** **Warncke**

105 Tergal discs, at least on T1, smooth and shiny, at most with very fine shagreenation...**106**

– Tergal discs shagreened or microreticulate, not strongly shiny, most dull and matt...**113**

106 Forewing with first submarginal cross vein separated from the stigma by three times its own width (Fig. 84E)...**107**

– Forewing with first submarginal cross vein separated from the stigma by more or less its own width (Fig. 84F)...**108**

107 Clypeus medially shagreened. Stigma dark brown. Sterna shagreened with the exception of the marginal zones. Common and widespread across Iberia... ***nana*** **(Kirby)**

– Clypeus medially shiny. Stigma bright, yellowish to reddish. Sternal discs shiny. Very rare, restricted to the Pyrenees.................. ***floricola*** **Eversmann**

108 Scutum densely shagreened, with large shallow 'crater-punctures'. In fresh specimens, T1–5 with broad white apical hair bands that exceed the length

of the marginal areas. S2–5 with distinct white apical hair bands. Restricted to mountainous areas of central and northern Spain .... ***argentata*** **Smith** (*partim*, small individuals)

– Scutum shiny or obscurely shiny, never densely shagreened, with normal punctures without raised rims. Terga and sterna without clear and dense complete hair bands **109**

109 Dorsal part of gena completely smooth and shiny, without any microsculpture. Discs of T2–4 very densely punctate, punctures separated by 0.5 puncture diameters. Restricted to dry and steppic habitats in central Iberia including northern Portugal.. ***bayona*** **Warncke**

– Gena uniformly shagreened, never with extensive smooth and shiny areas. Discs of T2–4 less densely punctate, punctures separated by at least 1 puncture diameter **110**

110 Antennae extensively lightened orange ventrally. T1 with very fine and scattered punctation. Rare, restricted to northern Spain, univoltine (August–September) .... ***nanula*** **Nylander**

– Antennae dark ventrally. T1 with clearer and denser punctation, punctures separated by 1–2 puncture diameters **111**

111 Terga with punctation clearly extending onto the depressed marginal areas. Genital capsule, see Fig. 84G. Associated with Cistaceae .... ***fabrella*** **Pérez**

– Terga with marginal areas essentially impunctate, at most with occasional puncture. Genital capsule otherwise... **112**

112 Marginal areas of T2–4 strongly depressed, mirror-smooth, without a single puncture. A4 as long as broad, equalling A3 in length. Found in the Sistema Central to west and north-western Iberia. Associated with *Sedum* (Crassulaceae).. ***omnilaevis*** **Wood**

– Marginal areas of T2–4 comparatively weakly depressed, smooth and shiny, but with occasional punctures. A4 subquadrate, broader than long, shorter than A3 in length. Widespread in Iberia .... ***alfkenella*** **Perkins**

113 A4 quadrate, as wide as long (Fig. 84H). Tergal margins strongly depressed and polished, mirror-smooth, impunctate. Restricted to the Pyrenees and Cantabrian Mountains.. ***semilaevis*** **Pérez**

– A4 subquadrate, broader than long. Tergal margins depressed or not......... **114**

114 Propodeal triangle laterally poorly defined, without clear carinae, internal surface with raised rugosity covering only central part in the form of a triangle, lateral parts therefore with granular shagreenation (Fig. 85A). Facial hair predominantly black. Clypeus usually smooth and shiny in its apical half. Terga essentially impunctate, regularly shagreened and dull, tergal margins weakly depressed. Univoltine (February–April) .... ***tenuistriata*** **Pérez**

– Without this exact combination of characters **115**

115 Scutum strongly shagreened and dull, very obscurely punctate, punctures separated by 2–4 puncture diameters, underlying surface matt; punctures often disappear into background sculpture..**116**

– Scutum less strongly shagreened to shiny, with at least some punctures clearly visible against the background sculpture; punctures separated by 1–2 puncture diameters **117**

116 Tergal discs finely shagreened and weakly shiny, with scattered punctures that are nevertheless distinct against the background sculpture, punctures separated by 1–3 puncture diameters. Tergal margins with finer shagreen, impunctate, thus contrasting the tergal discs. Restricted to temperate areas close to the Pyrenees ....***subopaca*** **Nylander**

– Tergal discs strongly shagreened and dull, with extremely obscure punctures that are hard to distinguish against the background sculpture, separated by 2–4 puncture diameters. Tergal margins with equally strong shagreen, not strongly contrasting the tergal discs. Iberian distribution unclear, but probably restricted to southern Spain (Cádiz, Málaga) ....***tiaretta*** **Warncke**

117 T1–3 with discs strongly and coarsely punctate, punctures clearly visible against the background sculpture (Fig. 85B). Tergal margins strongly depressed, finely shagreened, more or less shiny, thus strongly contrasting the tergal discs. Restricted to central and northern Spain, typically at altitude in mountainous areas ....***anthrisci*** **Blüthgen**

– T1–3 without strong and coarse punctures, at most with occasional punctures that typically disappear into the background sculpture. Tergal margins depressed or not, but not noticeably more finely sculptured or more brightly shiny than the tergal discs **118**

118 T2–4 with tergal margins strongly depressed **119**

– T2–4 with tergal margins at most weakly depressed..............................**120**

119 Scutum with scattered punctures, punctures separated by 1–3 puncture diameters. Mesopleuron finely microreticulate, punctate, punctures separated by >1 puncture diameter. Throughout Iberia, common[21]........................***spreta*** **Pérez**

– Scutum with denser punctures, punctures separated by 1–2 puncture diameters. Mesopleuron more coarsely microreticulate, punctate, punctures separated by <1 puncture diameter. Exact Iberian distribution unclear, but currently known only from eastern Spain, typically in mountainous areas[21]...***pauxilla*** **Stöckhert**

120 Scutum densely punctate, punctures typically separated by 1 puncture diameter. Scutum and scutellum shagreened and dull (1st generation) to weakly shiny (2nd generation). Genital capsule, see Fig. 85C..........***minutula*** **(Kirby)**

– Scutum more sparsely and irregularly punctate, punctures separated by 1–3 puncture diameters. Scutum and scutellum finely shagreened and weakly

21 The differentiation between these two species in Iberia in the male sex is not completely clear due to lack of available Iberian male material. Association with females should be made.

shiny (1st generation) to polished and shiny (2nd generation). Genital capsule, see Fig. 85D... ***minutuloides*** **Perkins**

121 (76) Mesepisternum and/or dorsolateral parts of the propodeum conspicuously punctate AND ocelloccipital distance at least 3 times the diameter of a lateral ocellus (*incisa*-group, *Pruinosandrena*) **122**

– Mesepisternum either impunctate or ocelloccipital distance of less than 3 times the diameter of a lateral ocellus..**126**

Figure 85. *Andrena* (*Micrandrena*) *tenuistriata* Pérez, 1895, male **A** propodeum, dorsal view; *Andrena* (*Micrandrena*) *anthrisci* Blüthgen, 1925, male **B** terga, dorsal view; *Andrena* (*Micrandrena*) *minutula* (Kirby, 1802), male **C** genital capsule, dorsal view; *Andrena* (*Micrandrena*) *minutuloides* Perkins, 1914, male **D** genital capsule, dorsal view; *Andrena* (*Pruinosandrena*) *nilotica* Warncke, 1975, male **E** genital capsule, dorsal view **F** *Andrena* (*Pruinosandrena*) *pruinosa* Erichson, 1835, male **F** genital capsule, dorsal view.

122 Dorsolateral parts of the propodeum impunctate, with dense network of raised rugosity...**123**

– Dorsolateral parts of the propodeum regularly punctate, without a dense network of raised rugosity..**124**

123 Face and mesosoma with a mixture of black and white pubescence. T2–4 laterally with widely separated patches of dense white pubescence on their apical margins that obscure the underlying surface. Terminal fringe black... .... ***lateralis*** **Morawitz**

– Face and mesosoma with light brown pubescence. T2–4 laterally without patches of white pubescence, at most with obscure whitish hair bands. Terminal fringe light brown..***incisa*** **Eversmann**

124 A3 exceeding A4+5 in length..***parata*** **Warncke**

– A3 not exceeding A4+5..**125**

125 Genital capsule without clear kink in the inner margins of the gonostyli (Fig. 85E). Scutum less densely punctate, punctures separated by 0.5 puncture diameters, with shiny interspaces, predominantly shiny...................... .... ***nilotica*** **Warncke**

– Genital capsule with clear kink in the inner margins of the gonostyli (Fig. 85F). Scutum more densely punctate, punctures almost confluent, predominantly dull..***pruinosa*** **Erichson**

126 (121) Clypeus flattened over majority of its surface (subgenus *Taeniandrena*)[22] **127**

– Clypeus not noticeably flattened...**139**

127 Genital capsule with pronounced gonocoxal teeth, these clearly projecting anteriorly for a distance greater than the diameter of an antenna (Fig. 86A, B) **128**

– Genital capsule with at most weakly projecting gonocoxal teeth (Fig. 86C–F)...**129**

128 Penis valves more or less parallel-sided (Fig. 86A). Gonostyli basally (before flattened apical parts) with dense network of longitudinal striations on their dorsal surface. Known only from central Portugal (Castelo Branco) and south-western Spain (Huelva, Cádiz). Flying early in the season (March–April).. ***lusitania*** **Wood & Ortiz-Sánchez**

– Penis valves very broad basally, occupying almost entire space between gonostyli (Fig. 86B). Gonostyli without longitudinal striations on their dorsal surface. Restricted to northern Spain. Flying slightly later (April–June) .... ***lathyri*** **Alfken**

22 Males of this subgenus are highly challenging and in some cases impossible to identify. There are several outstanding taxonomic issues in this subgenus that require in-depth genetic study to resolve, and additional probably undescribed cryptic species are present. Do not expect to identify this group without consulting confidently determined reference material, and ideally barcoded specimens. Minimal characters are given here because of the ongoing lack of taxonomic clarity in this subgenus.

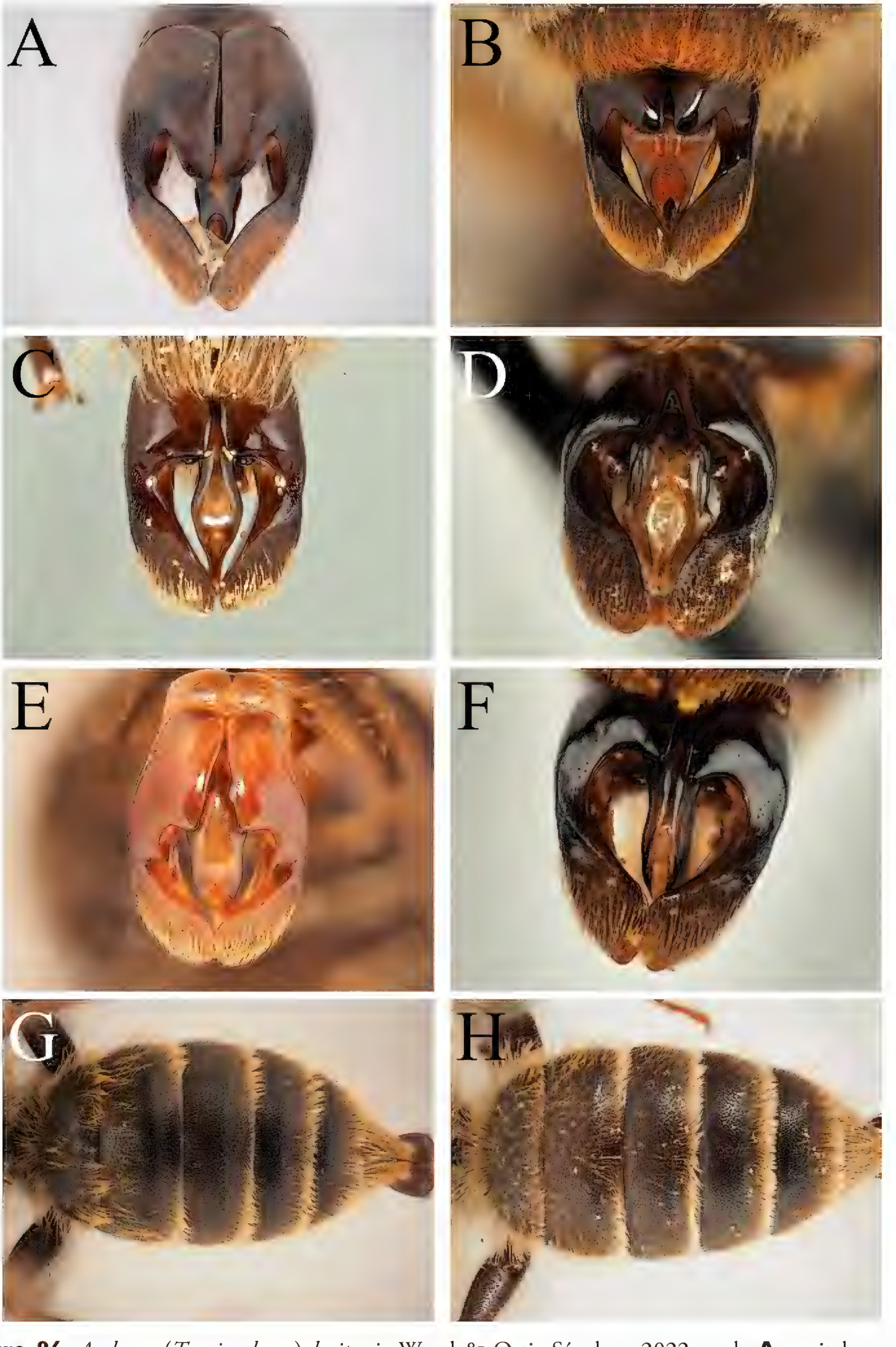

Figure 86. *Andrena* (*Taeniandrena*) *lusitania* Wood & Ortiz-Sánchez, 2022, male **A** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *lathyri* Alfken, 1900, male **B** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *gredana* Warncke, 1975, male **C** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *intermedia* Thomson, 1870 aggregate, male **D** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *levante* Wood & Praz, 2021, male **E** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *contracta* Wood, 2022, male **F** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *wilkella* (Kirby, 1802), male **G** terga, dorsal view; *Andrena* (*Taeniandrena*) *benoisti* Wood & Praz, 2021, male **H** terga, dorsal view.

129 Genital capsule with penis valves narrow basally, broad medially, and narrowing apically (Fig. 86C). Restricted to the Sistema Central and northern and western Iberia.. ***gredana* Warncke**

– Genital capsule different **130**

130 Penis valves broadened and gonocoxae with their inner margins diverging from their base, gonocoxae therefore forming a broad triangular opening basally (Fig. 86D, E) **131**

– Penis valves not broadened or gonocoxae with their inner margins more or less parallel, sometimes slightly diverging apically **132**

131 Penis valves strongly broadened, occupying the majority of the space between the gonostyli (Fig. 86D). Gonostyli with strongly raised inner margin, this forming a distinct obtuse angle medially. Found across mountainous areas in eastern Spain.................................... ***intermedia* Thomson aggregate** (this likely represents a complex of an unknown number of species, potentially all of which are undescribed; the true *intermedia* may be absent from Spain)

– Penis valves not so strongly broadened, occupying ½ the space between the gonostyli (Fig. 86E). Gonostyli with weakly raised inner margin, not presenting a distinct angle. Restricted to southern and south-eastern Spain (Almería, Granada, Málaga, Murcia, Valencia). Univoltine (April–June) .... ***levante* Wood & Praz**

132 Genital capsule with weakly produced gonocoxal teeth (Fig. 86F). Penis valves very narrow, more or less parallel-sided. Restricted to the alpine zone of the Sierra Nevada (typically above 2000 m) .... ***contracta* Wood**

– Genital capsule different, species found elsewhere................................ **133**

133 A3 short relative to A4, approximately 0.6–0.7 times as long................ **134**

– A3 long, more or less as long as A4, typically between 0.8–1.2 times as long **136**

134 Clypeus densely covered with snow-white vestiture, in fresh specimens completely obscuring the underlying surface, particularly of the apical margin. Terga strongly shagreened, punctation obscure, T1 with declivity almost impunctate, any punctures sparse and obscure. Marginal areas of T2–4 almost impunctate. Currently known only from the steppe of central Spain (Guadalajara, Salamanca, Segovia). Univoltine (May–June) .... ***ovata* Schenck**

– Clypeus without such pubescence, the surface of the clypeus is usually clearly visible through the sparser pubescence. Terga with stronger more distinct punctation, including declivity of T1. Marginal areas of T2–4 distinctly punctate, at least basally.. **135**

135 Terga with weak apical hair bands, widely interrupted on T2–3, complete on T4 (Fig. 86G). Smaller, 8–9 mm. Restricted to northern Portugal and Spain to the Pyrenees with isolated populations at elevation in the Sistema Central and Sistema Ibérico .... ***wilkella* (Kirby)**

– Terga with strong and thick apical hair bands, medially interrupted on T2, complete on T3–4 (Fig. 86H). Larger, 10–11 mm. Restricted to the Sistema Central to central and northern Portugal and north-western Spain

(Zamora). Not known from the Pyrenees or Cantabrian Mountains........... .... ***benoisti* Wood & Praz**

136 Hind tibiae and basitarsi lightened orange. Terga strongly shagreened, usually with punctures obscure and disappearing into underlying sculpture. A3 sometimes a little longer than A4. Larger, 10–12 mm. Univoltine (April–June) .....***russula* Lepeletier sensu lato** (including the distinct mitochondrial lineage from southern Portugal)

– Hind legs usually dark. Terga variable, often with abundant and distinct punctures. A3 variable. Smaller, 8–10 mm. Bivoltine (March-August) 137

137 A3 often shorter than A4 (Fig. 87E). Genital capsule with gonostyli produced into apical points (Fig. 87F). Currently only confirmed from the coast of southern Spain (Málaga). Bivoltine (probably February–April; May–June)[23] ....***poupillieri* Dours**

– Genital capsule with gonostyli apically truncate, not produced into points. **138**

138 A4 usually equal or subequal to A3 in length (Fig. 87A). Terga less densely punctate, surface more finely shagreened, weakly shiny. Genital capsule comparatively less elongate, gonostyli broad with external margin usually straight (Fig. 87B). Internal margins of gonocoxae slightly divergent apically. Penis valve slightly broader basally. Throughout Iberia. Bivoltine (typically May–June; July–August) .... ***afzeliella* (Kirby)**

– A4 often slightly longer than A3 (Fig. 87C). Terga more densely punctate, shagreened and matt. Genital capsule comparatively more slender, gonostyli narrower, external margin weakly concave (Fig. 87D). Internal margins of gonocoxae usually parallel apically. Penis valve on average slightly narrower basally. Widespread throughout Iberia, most common in areas with an Atlantic climate and abundant Genisteae. Bivoltine (typically March–May; June–July)..***ovatula* (Kirby)**

139 (126) At least some tergal discs red-marked (Fig. 41G) **140**

– Tergal discs never red-marked, at most with tergal margins lightened **144**

140 A3 longer than A4 ....**141**

– A3 much shorter than A4, at most ¼ the length **143**

141 Head broad, inner margin of compound eyes diverging ventrally (Fig. 41F). Pronotum with strong humeral angle. Clypeus smooth and shiny with scattered punctures. Genital capsule unique, elongate, gonocoxae truncate with inner margin rounded, penis valves basally broad, strongly narrowing medially to become elongate and acutely pointed apically (Fig. 41H)................ ....***florea* Fabricius**

– Without this combination of characters..**142**

23 These three taxa are extremely challenging to separate in the male sex. Comparison to confidently determined or preferably barcoded specimens should be made, as well as association with females.

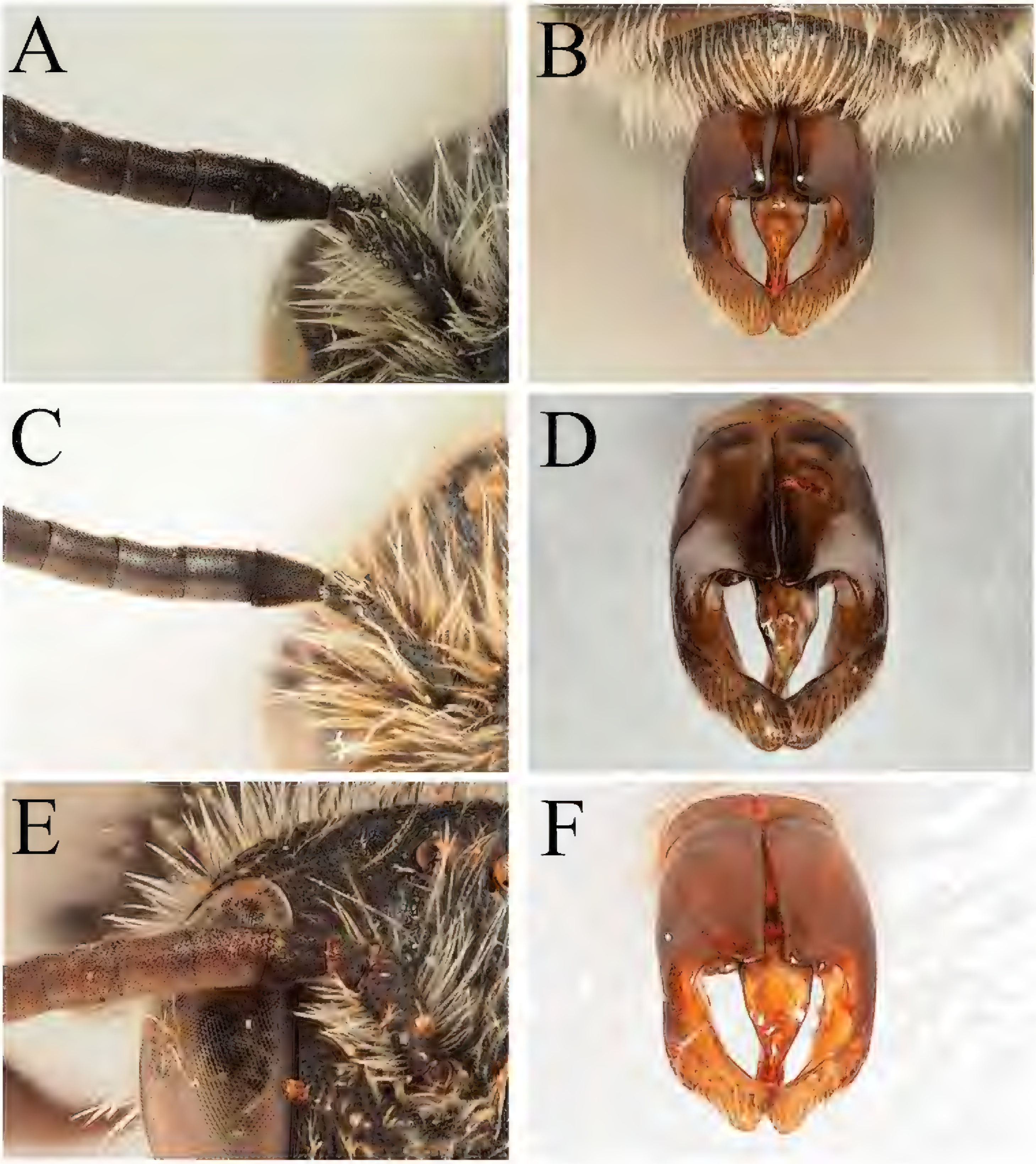

Figure 87. *Andrena* (*Taeniandrena*) *afzeliella* (Kirby, 1802), male **A** antennae, frontal view **B** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *ovatula* (Kirby, 1802), male **C** antennae, frontal view **D** genital capsule, dorsal view; *Andrena* (*Taeniandrena*) *poupillieri* Dours, 1872, male **E** antennae, frontal view **F** genital capsule, dorsal view.

142 Clypeus shagreened and matt. Mesonotum and disc of T1 strongly and densely punctate. Hind basitarsi lightened orange. Restricted to the Pyrenees, associated with *Campanula* (Campanulaceae) .... ***rufizona* Imhoff**

– Clypeus smooth and shiny. Mesonotum and disc of T1 weakly punctate with scattered punctures. Hind basitarsi dark. More widespread across Spain .... ***parviceps* Kriechbaumer** (*partim*, light form)

143 S8 apically truncate, lacking apical emargination. Mandibles always bidentate .... ***rosae*** **Panzer** (*partim*, light form)

– S8 with clear apical emargination. Mandibles unidentate (1st generation) or bidentate (2nd generation) .... ***trimmerana*** **(Kirby)** (*partim*, light form)

144 (139) Tergal discs with metallic blue reflections........ **145**

– Tergal discs dark, without metallic reflections, or at most with greasy greenish or bronzy reflections laterally (if greenish reflections present on clypeus, scutum, and scutellum, go to couplet 182), never with blue metallic reflections........ **147**

145 Tergal discs with abundant 'crater punctures' with raised rims. Pubescence of mesosoma and face light brown, never with abundant black and white hairs........ ***nigroolivacea*** **Dours**

– Tergal discs with simple punctures, without noticeably raised rims. Pubescence of mesosoma with abundant black and white hairs, on the mesosoma forming a striped pattern; white anteriorly and posteriorly, medially with a uniform black strip........ **146**

146 A3 0.6 times as long as A4. Facial hair shorter than the width of a compound eye. Antennal scape with intermixed black and white hairs. Bivoltine (April–May; July–August), restricted to mountains in northern Spain and the Pyrenees[24] .... ***barbareae*** **Panzer**

– A3 as long or almost as long as A4. Facial hair exceeding the width of a compound eye. Antennal scape with uniformly white hairs. Univoltine (April–May), more widespread across northern Portugal and Spain[24] ... ***cineraria*** **(Linnaeus)**

147 (144) Mandibles elongate, sickle-like, strongly crossing apically (Fig. 88A). Pronotum with strong humeral angle. Gena often expanded, broader than the width of a compound eye........ **148**

– Without this combination of characters; mandibles normal, not elongate and strongly crossing apically (Fig. 88B). Pronotum usually without a strong humeral angle. Gena usually normal, equalling or shorter than the width of a compound eye........ **167**

148 Genital capsule distinctive, gonostyli long and filiform, penis valves grossly expanded, occupying almost the entire space between the gonostyli (Fig. 88C). S8 elongate and strongly emarginate medially, forming a 'Y' shape. Rare, restricted to the Pyrenees........ ***bucephala*** **Stephens**

– Genital capsule and S8 otherwise........ **149**

149 A3 extremely short, at most ¼ the length of A4........ **150**

– A3 longer, never this short. If in doubt, then terga with well-defined and narrow light brown apical hair bands........ **153**

150 S8 apically truncate, lacking apical emargination. Mandibles always bidentate .... ***rosae*** **Panzer** (*partim*, dark form)

– S8 with clear apical emargination. Mandibles either unidentate or bidentate **151**

24 These two species are challenging to separate morphologically.

151 Mandible unidentate, lacking an inner subapical tooth. Gena usually with a long spine. Flying only in the spring (March-May, depending on elevation).................... ***trimmerana*** **(Kirby)** (*partim*, dark form, 1st generation)

– Mandible bidentate, with an inner subapical tooth. Gena usually without a spine, sometimes with a very short spine. Flying in the spring or the summer **152**

152 Flying in the spring (usually April to mid-June). Facial pubescence long. Rare, restricted to cooler parts of Iberia.............................. ***scotica*** **Perkins**

– Flying in the summer (usually mid-June to July). Facial pubescence short. Widespread throughout Iberia ....
.... ***trimmerana*** **(Kirby)** (*partim*, dark form, 2nd generation)

153 Mandible unidentate, without inner subapical tooth. Sometimes there may be a hint of a weakly formed or ancient subapical tooth; this state should be treated as unidentate. Head often grossly enlarged **154**

– Mandible clearly bidentate, with a strong inner subapical tooth. Head not normally grossly enlarged..**156**

154 A3 slightly shorter than A4. Clypeus in apical third bulging, surface smooth and shiny with scattered punctures, punctures separated by 1–4 puncture diameters. Hind tibiae and tarsi usually lightened orange. Northern and central Spain, in areas with deciduous forest. Associated with *Quercus* (Fagaceae) .... ***ferox*** **Smith**

– A3 clearly longer than A4. Clypeus even, without bulging apical part, underlying surface evenly shagreened and regularly punctate. Hind tibiae and tarsi dark...**155**

155 Clypeus densely punctate, punctures separated by 0.5–1 puncture diameter. Clypeus apically occasionally with very small pale marking medially. Tergal discs with scattered punctures, punctures separated by 2–3 puncture diameters, underlying surface smooth and shiny. Bivoltine, flying April-May and again July-August[25] .... ***nuptialis*** **Pérez**

– Clypeus with sparser punctures, punctures separated by 1–2 puncture diameters. Tergal discs densely punctate, punctures separated by 1–2 puncture diameters, underlying surface shagreened, weakly shiny. Univoltine, typically flying March-June depending on altitude[25] .... ***vetula*** **Lepeletier**

156 A3 distinctly shorter than A4. Genital capsule with gonocoxal teeth pronounced but strongly truncate apically, quadrangular (Fig. 88D). Terga with well-defined and narrow apical light brown hair bands, these occupying only the apical part of the marginal areas (Fig. 88E) .... ***leptopyga*** **Pérez**

– A3 at least as long as A4, usually longer. Genital capsule either with less strongly pronounced gonocoxal teeth, or with gonocoxal teeth apically rounded. Terga with or without apical tergal hair bands........................**157**

25 These two species are unrelated, but have converged on a quite similar morphology; more care is required than might be expected based on their divergent female morphology.

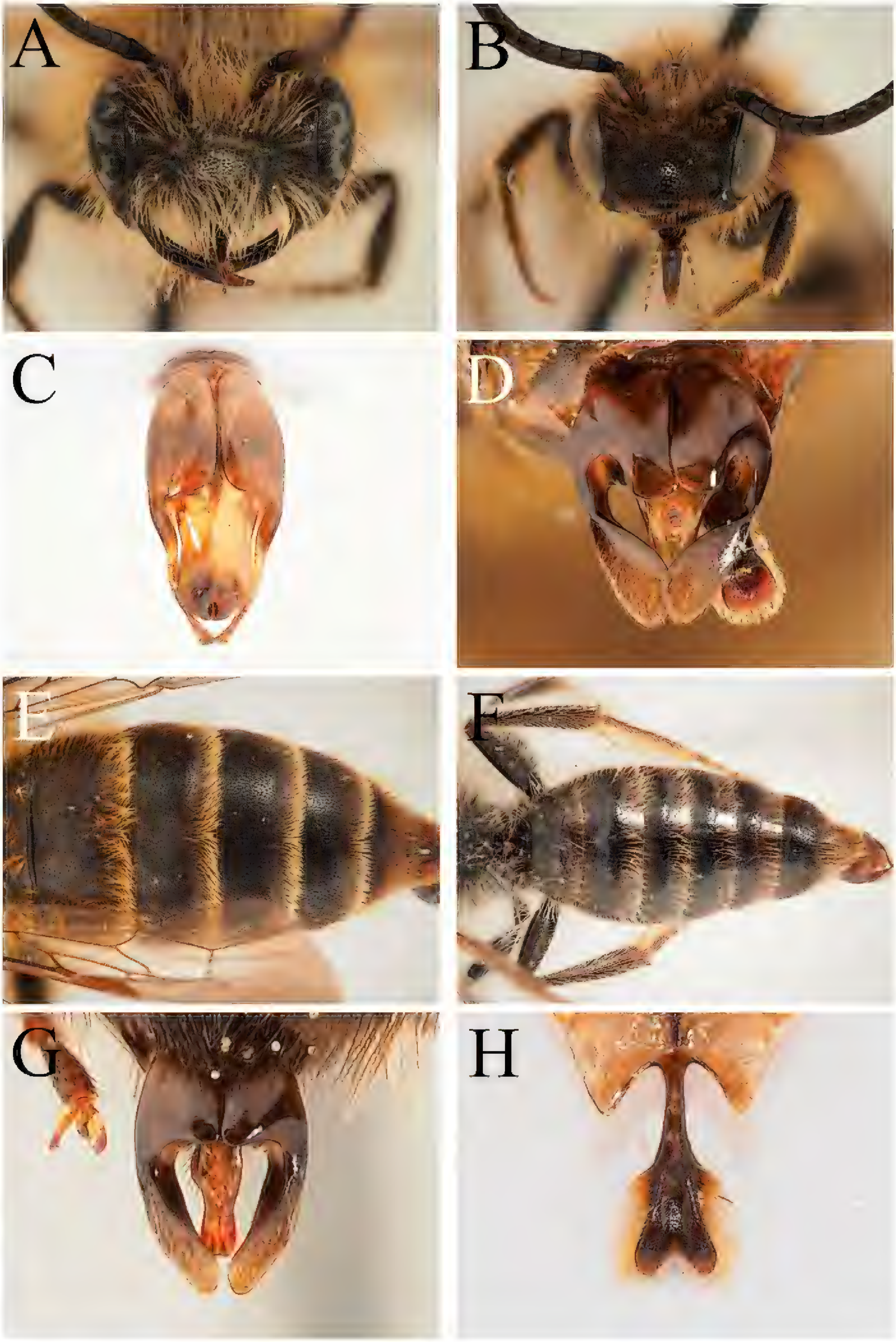

Figure 88. *Andrena* (*Andrena*) *helvola* (Linnaeus, 1758), male **A** head, frontal view; *Andrena* (*Chrysandrena*) *fulvago* (Christ, 1791), male **B** head, frontal view; *Andrena* (*Hoplandrena*) *bucephala* Stephens, 1846, male **C** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *leptopyga* Pérez, 1895, male **D** genital capsule, dorsal view **E** terga, dorsal view; *Andrena* (*Euandrena*) *angustior* (Kirby, 1802), male **F** tergal, dorsal view; *Andrena* (*Euandrena*) *lavandulae* Pérez, 1902, male **G** genital capsule, dorsal view; *Andrena* (*Lepidandrena*) *paucisquama* Noskiewicz, 1924, male **H** S8, dorsal view.

157 Marginal area of T2 broad, occupying ½ the length of the segment, strongly depressed, surface smooth and shiny (Fig. 88F). Found in areas with a temperate Atlantic climate across central, north-western, and northern Iberia..***angustior* (Kirby)**

– Marginal area of T2 never this broad; at most weakly depressed, surface structurally not clearly differentiated from the disc, never smooth and shiny...**158**

158 Genital capsule with gonocoxae apically rounded, gonocoxal teeth very slightly protruding at most (Fig. 88G). Facial pubescence intermixed light brown and black, brown medially, black apically and laterally. Usually smaller, 8–9 mm. Found in areas with a Mediterranean climate ....***lavandulae* Pérez**

– Genital capsule with more strongly projecting gonocoxal teeth, overall capsule more robustly built. Facial pubescence either black or pale, never mixed. Usually larger, 9–12 mm. Typically not found in areas with a Mediterranean climate, species of temperate deciduous forest (subgenus *Andrena* s. str.)..**159**

159 Mandible at its base with a clearly pronounced tooth............................**160**

– Mandible at its base with either an angulation or straight **165**

160 A3 1.8 times longer than A4. Hind tarsi lightened orange. With a patchy distribution from northern Portugal and Spain to the Pyrenees, with an isolated population in the Sierra de Cazorla (Jáen)..............***fulva* (Müller)**

– A3 at most 1.3 times longer than A4, usually more or less equal in length. Hind tarsi dark to reddish...**161**

161 Propodeum with majority of hairs black, at most with scattered pale hairs.. ....**162**

– Propodeum with majority of hairs pale, at most with scattered dark hairs... ....**163**

162 S8 apically emarginate. Slightly smaller, 9–11 mm.........***praecox* (Scopoli)**

– S8 apically truncate. Slightly larger, 10–12 mm..................***apicata* Smith**

163 Basal mandibular tooth short. Apical margins of S2–4 with long loose hairs that do not form clear fringes, hairs longer than the length of the hind basitarsis. Restricted to northern Spain. Flying later in the year (June–August), associated with shrubs, particularly *Rubus* (Rosaceae)............***fucata* Smith**

– Basal mandibular tooth long. Apical margins of S2–4 with dense fringes composed of short hairs, these hairs not exceeding the length of the hind basitarsis. Flying earlier in the year (March-June).................................**164**

164 Hind tarsi reddish. Genital capsule more elongate, gonocoxal teeth comparatively weak. Restricted to areas around the Pyrenees and Cantabrian Mountains. Flying during March-May, associated with *Salix* (Salicaceae) ... .***mitis* Schmiedeknecht**

– Hind tarsi dark. Genital capsule more compact, gonocoxal teeth strongly produced. More widespread across northern Iberia into northern Portugal. Flying during May-June, associated with *Vaccinium* (Ericaceae)................. ....***lapponica* Zetterstedt**

165 Mandible without any kind of angulation at its base. Mesosoma with bright reddish brown hairs, with some black hairs on the mesepisternum. Associated with *Salix* (Salicaceae) ....***clarkella* (Kirby)**

– Mandible at its base with an angulation. Mesosoma never with black hairs laterally. Associated with a wider range of flowering trees and shrubs........**166**

166 Mandible at its base with angulation forming a strong 90° angle. In fresh specimens, clypeus with golden hairs. Terga with marginal areas normal, marginal area of T3 occupying at most 30% of segment length. Restricted to the Pyrenees with an isolated population in the Sierra de Cazorla (Jáen) ....***helvola* (Linnaeus)**

– Mandible at its base with angulation rounded, forming an obtuse angle (c. 120°). In fresh specimens, clypeus with white hairs. Terga with marginal areas broad, marginal area of T3 occupying 60% of segment length. More widespread across central and northern Iberia into northern Portugal .... ***synadelpha* Perkins**

167 (147) Measured along ventral margin, A3 twice as long as A4 ....**168**

– Measured along ventral margin, A3 longer or shorter than A4, but never twice as long **193**

168 S8 unique, elongate on narrow step, apical portion medially constricted and apically strongly emarginate (Fig. 88H) ....***paucisquama* Noskiewicz**

– S8 different, not of this shape **169**

169 Fore margin of the clypeus upturned. Propodeal triangle broad and well-defined by raised lateral carinae, margins extending almost to the lateral edges of the metanotum, internal surface covered in raised irregular carinae of a similar width, thus appearing regular and consistent. Pronotum with weak or strong humeral angle. Genital capsule, see Fig. 45E, F (subgenus *Ovandrena*).....**170**

– Without this combination of characters...**171**

170 Larger, 9–10 mm. Tongue with outer surface of galea clearly punctate, punctures separated by 1–2 puncture diameters. Pronotum with humeral angle comparatively weak, and fore margin of the clypeus only weakly upturned. Sterna with weak and sparse fringes on apical margins. Tergal punctation comparatively larger and coarser. Genital capsule, see Fig. 45F ....***oviventris* Pérez**

– Smaller, 7–8 mm. Tongue with outer surface of galea more or less smooth and shiny, without obvious punctures. Pronotum with humeral angle comparatively strong, and fore margin of the clypeus more strongly upturned. Sterna with strong and dense fringes on apical margins. Tergal punctation comparatively fine. Genital capsule, see Fig. 45E ....***farinosa* Pérez**

171 Clypeus smooth and shiny over almost its entire surface, regularly punctate, punctures separated by 0.5–1 puncture diameters. Metasoma elongate, essentially parallel-sided, surface finely shagreened, more or less smooth and shiny, deeply punctate, punctures separated by 0.5–2 puncture diameters. Genital capsule with gonocoxal teeth apically diverging (Fig. 89A) ....***alluaudi* Benoist**

– Without this combination of characters...**172**

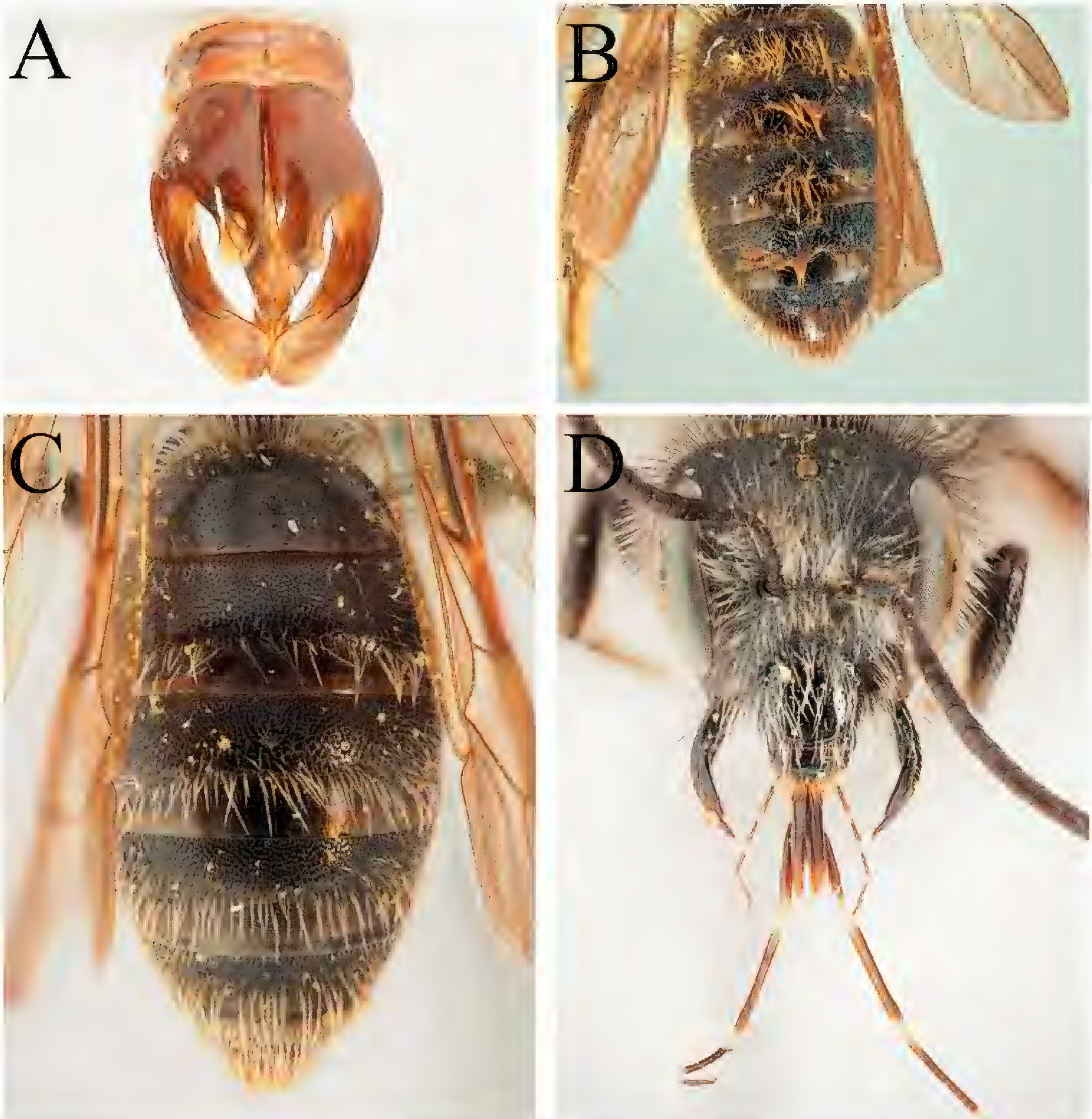

Figure 89. *Andrena* (incertae sedis) *alluaudi* Benoist, 1961, male **A** genital capsule, dorsal view; *Andrena* (*Euandrena*) *fortipunctata* Wood, 2021, male **B** terga, dorsal view; *Andrena* (*Aenandrena*) *hystrix* Schmiedeknecht, 1883, male **C** terga, dorsal view **D** *Andrena* (*Euandrena*) *solenopalpa* Benoist, 1945, male **D** face, frontal view.

172 Tergal margins distinctly depressed, medially occupying 40% of the visible segment (Fig. 89B, C). Tergal discs densely punctate, punctures separated by 0.5–1 puncture diameters; tergal margins impunctate, lightened hyaline brown, strongly contrasting tergal discs..**173**

– Tergal margins either not depressed, not impunctate, not lightened hyaline brown, or narrower...**174**

173 Tergal discs strongly humped, accentuating contrast with margins (Fig. 89B). Margins of T2–4 with irregular light brown hairs. Facial pubescence medially light brown, laterally black along the inner margins of the compound

eyes. Terga never lightened reddish laterally. Known only from mountainous areas in north-western, central, and south-eastern Spain (Léon, Ávila, Jáen) .... ***fortipunctata* Wood**

– Tergal discs not strongly humped (Fig. 89C). Margins of T2–4 basally with long whitish plumose hairs that arise from the junctions with the discs and overly the marginal areas without obscuring the underlying surface. Facial pubescence uniformly whitish. Terga often reddish laterally, view in profile. Widespread across Iberia .... ***hystrix* Schmiedeknecht** (*partim*)

174 Head elongate, mouthparts extremely long, twice the length of the head, labial palps alone equal the length of the head (Fig. 89D). Associated with *Lithodora* (Boraginaceae).. ***solenopalpa* Benoist**

– Head shorter, never with the labial palps equalling the length of the head... .... **175**

175 Gonostyli with outer margin concave, penis valves with weak lateral hyaline extensions (Fig. 90A). Terga strongly microreticulate, dull. Clypeus medially with unclear and slightly raised impunctate midline, otherwise densely punctate, underlying surface largely smooth and shiny. Restricted to areas close to the Pyrenees. Associated with *Symphytum* (Boraginaceae).............. .... ***symphyti* Schmiedeknecht**

– Without this combination of characters.. **176**

176 A4–13 ventrally covered with shiny scales, contrasting A3 which is ventrally dull (c.f. Fig. 88B). Tergal margins widely lightened yellow-orange hyaline. Scutellum with intermixed brown-orange and black hairs. Terga very finely shagreened, more or less smoothly shiny, regularly punctate, punctures separated by 1–2 puncture diameters... ***fertoni* Pérez**

– Without this combination of characters.. **177**

177 Face with pale hairs medially and black hairs along the inner margin of the compound eyes. Genital capsule with surface of the gonocoxae with distinctive latitudinal granular shagreen, this extending onto the basal parts of the gonostyli (Fig. 90B–D). Terga shagreened, with large scattered punctures on tergal discs, these almost becoming crater-like on T1, but without clearly raised rims. (former subgenus *Zonandrena*, *partim*).............................. **178**

– Without this combination of characters (for species with contrasting black hairs along the inner margin of the compound eyes, see the next couplet) **181**

178 Genital capsule with outer margins of gonostyli weakly emarginate (Fig. 90B, C) **179**

– Genital capsule with outer margins of gonostyli more or less straight, without emargination (Figs 15B–D, 90D)... **180**

179 Penis valves comparatively broad (Fig. 90B). Rare, restricted to the Pyrenees.. ***gravida* Imhoff** (*partim*)

– Penis valves comparatively narrow (Fig. 90C). Restricted to steppic areas in central Spain.. ***soror* Dours**

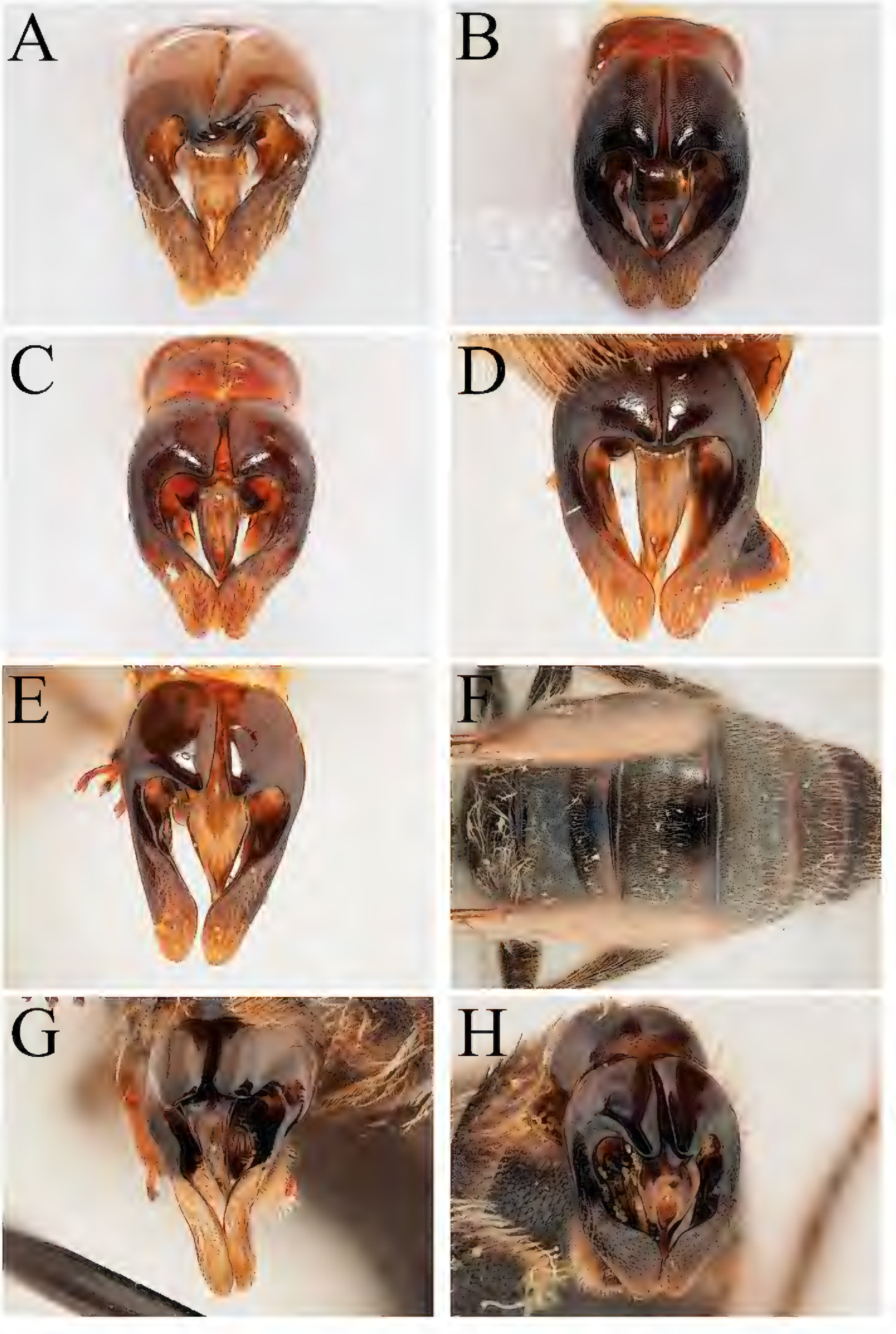

Figure 90. *Andrena* (*Euandrena*) *symphyti* Schmiedeknecht, 1883, male **A** genital capsule, dorsal view; *Andrena* (*Melandrena*) *gravida* Imhoff, 1832, male **B** genital capsule, dorsal view; *Andrena* (*Melandrena*) *soror* Dours, 1872, male **C** genital capsule, dorsal view; *Andrena* (*Melandrena*) *vulcana* Dours, 1873, male **D** genital capsule, dorsal view; *Andrena* (*Melandrena*) *bicolorata* (Rossi, 1790), male **E** genital capsule, dorsal view; **F** terga, dorsal view; *Andrena* (*Lepidandrena*) *baetica* Wood, 2020, male **G** genital capsule, dorsal view; *Andrena* (*Lepidandrena*) *pandellei* Pérez, 1895, male **H** genital capsule, dorsal view.

180 Genital capsule with penis valves comparatively narrow (Fig. 90D). Terga microreticulate, dull to weakly shiny. Punctures on disc of T2 less visible against background sculpture[26] .... ***vulcana* Dours**

– Genital capsule with penis valves comparatively broad (Fig. 15B–D). Terga shagreened, weakly shiny. Punctures on disc of T2 more clearly visible against weaker background sculpture[26] .... ***discors* Erichson**

181 Face predominantly white-haired, with black hairs along inner margin of compound eyes. Genital capsule elongate, relatively featureless (Fig. 90E). Tergal discs densely and finely punctate, punctures separated by 0.5 puncture diameters (Fig. 90F). Tergal margins slightly but distinctly depressed, with small, fine, and obscure punctures, the margins thus strongly contrasting the discs; underlying surface finely shagreened and weakly shiny **182**

– Without this combination of characters 183

182 Tergal discs with uniformly pale pubescence (Fig. 90F)........ ***bicolorata* (Rossi)**

– Tergal discs with intermixed black and white pubescence........................... .... ***florentina* Magretti**

183 Terga densely and regularly punctate, punctures separated by up to 1 puncture diameter, underlying surface weakly shagreened to smooth and shiny. T2–4 with distinct white apical hair bands, often abraded and interrupted medially (remaining *Lepidandrena*) **184**

– Terga shagreened, with large 'crater punctures' with raised rims. Tergal margins without apical hair bands (remaining *Chlorandrena*) **186**

184 Genital capsule elongate, gonostyli extremely long, many times longer than wide (Fig. 90G). Hind basitarsi lightened orange.................. ***baetica* Wood**

– Genital capsule with gonostyli compact, not extremely narrow and elongate (Fig. 90H). Hind basitarsi dark...**185**

185 S8 with short hairs that do not noticeably project laterally. Tarsal segment 5 of the hind leg elongate and bent. Slightly larger, 10–11 mm .... ***curvungula* Thomson**

– S8 with long, laterally projecting hairs. Tarsal segment 5 of the hind leg not noticeably bent. Slightly smaller, 9–10 mm .... ***pandellei* Pérez**

186 Process of S8 large, with triangular-shaped lateral projections covered with projecting hair tufts (Fig. 91A; *taraxaci*-group) **187**

– Process of S8 large or small, but more or less parallel-sided, without triangular lateral projections or hair tufts (Fig. 91B–D) **189**

187 Ventral surface of S8 with long, ventrally projecting hairs, clearly visible in profile. Apex of S8 emarginate .... ***senecionis* Pérez**

– Ventral surface of S8 without ventrally projecting hairs. Apex of S8 rounded, never medially emarginate..**188**

26 Separation of the these species is very challenging without access to confidently determined reference material.

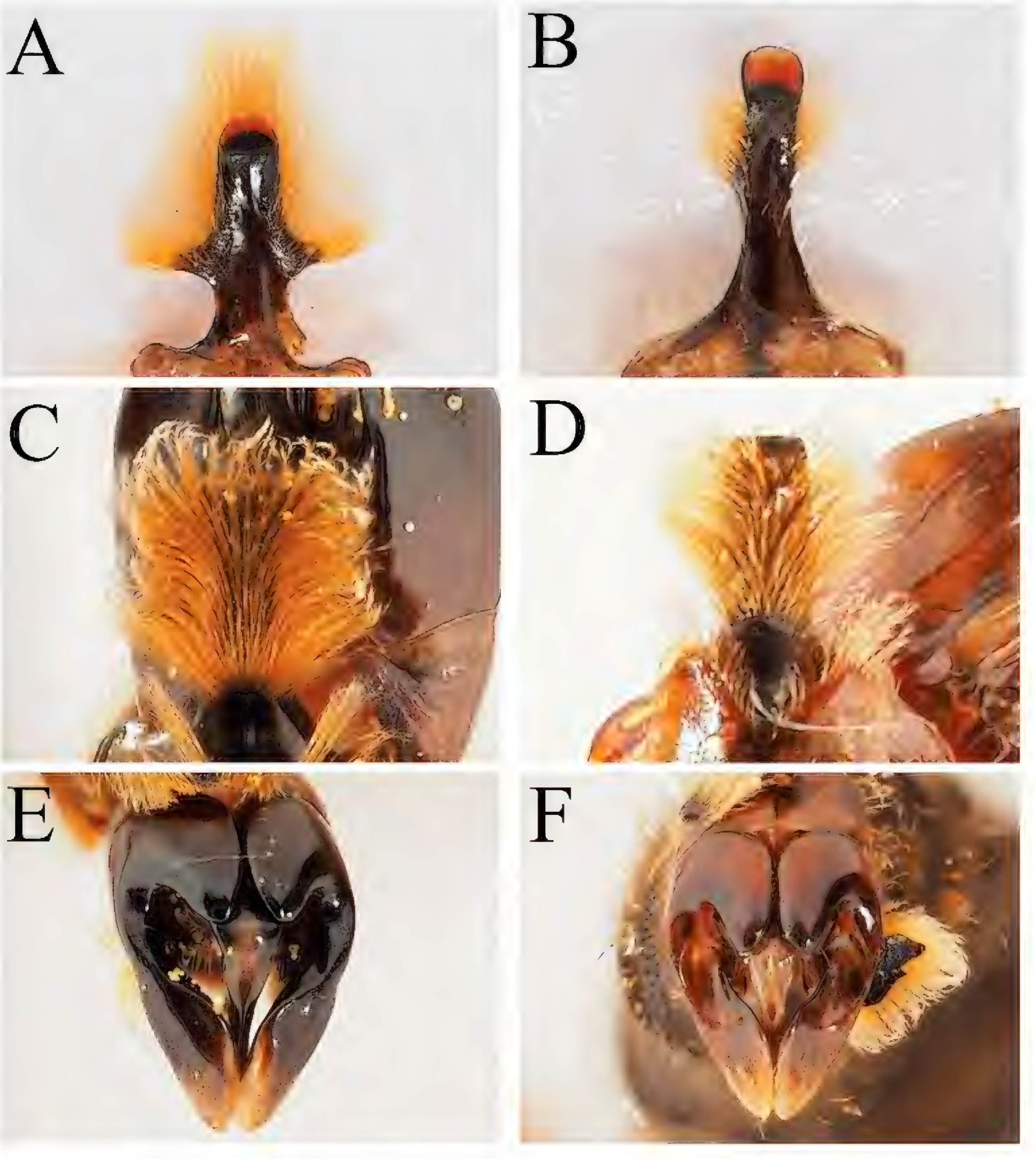

Figure 91. *Andrena* (*Chlorandrena*) *rhenana* Stöckhert, 1930, male **A** S8, dorsal view; *Andrena* (*Chlorandrena*) *cinerea* Brullé, 1832, male **B** S8, dorsal view; *Andrena* (*Chlorandrena*) *livens* Pérez, 1895, male **C** S8, ventral view **E** genital capsule, dorsal view; *Andrena* (*Chlorandrena*) *abrupta* Warncke, 1967, male **D** S8, ventral view; *Andrena* (*Chlorandrena*) *agnata* Warncke, 1967, male **F** genital capsule, dorsal view.

188 Apex of gonostyli with dense, deeply impressed punctuation, gonocoxal lobes strongly pronounced, apically pointed. Common throughout Iberia.. ....***rhenana* Stöckhert**

– Punctuation of gonostyli scattered, especially on the rim of the inner margin, gonocoxal lobes smaller, apexes broadly rounded. Rare, southern and south-eastern Spain only .... ***curtivalvis* Morice**

189 Process of S8 relatively short, ventral surface apically glabrous, viewed ventrally with hairs covering an area more or less as broad as long (Fig. 91B) ... . ***cinerea*** **Brullé**

– Process of S8 relatively long, ventral surface entirely covered with hairs, viewed ventrally with hairs covering an area clearly longer than broad (Fig. 91C, D) **190**

190 Larger, 11–12 mm. S8 strongly broadened apically, here broader than the stem (Fig. 91C). Body dark, without metallic reflections **191**

– Smaller, 9–10 mm. S8 parallel-sided along its entire length, not apically broadened (Fig. 91D). Clypeus, scutum, scutellum, and tergal discs with obscure greasy green metallic reflections.. **192**

191 Gonostyli with inner margins more or less evenly rounded (Fig. 91E). Terga comparatively more strongly shagreened, weakly shiny. Distributed throughout Iberia .... ***livens*** **Pérez**

– Gonostyli with inner margins strongly flattened and produced into a raised ridge (Fig. 91F). Terga with shagreenation reduced, terga more strongly shiny in direct comparison. Rare, known only from as single specimen captured near to Madrid ....***agnata*** **Warncke**

192 Clypeus strongly domed, underlying surface weakly shagreened laterally, smooth and shiny over the majority of its area; clypeus largely dark, with at most occasional hints of metallic green reflections. Terga with bases very weakly depressed. Found in dry to steppic areas in central Spain ....***elata*** **Warncke**

– Clypeus weakly domed, underlying surface shagreened, weakly shiny; metallic green reflections present. Terga with bases strongly depressed. Found in areas close to or on the coast in southern Portugal and Spain.................. ....***abrupta*** **Warncke**

193 (167) Measured along ventral margin, A3 shorter than or as long as A4 ....**194**

– Measured along ventral margin, A3 slightly longer than A4 ....**215**

194 A3 extremely short relative to A4, at most $^{1}/_{5}$ the length (Fig. 81A). Terga dark. Genital capsule distinctive, with extremely narrow parallel-sided penis valves (Fig. 81B). Rare, known from eastern Spain (Jáen, Soria, Teruel)...... .... ***vaulogeri*** **Pérez** (*partim*, normal sized individuals)

– Without this combination of characters...**195**

195 Fore margin of clypeus upturned. Gena slightly exceeding width of compound eye. T2–4 with dense white apical hair bands (Fig. 40G). Genital capsule compact, rounded, with gonocoxal teeth apically diverging, gonostyli apically broadened and flattened (Fig. 40H) ....***blanda*** **Pérez**

– Without this combination of characters...**196**

196 A4–13 ventrally covered with shiny scales, contrasting A3 which is ventrally dull (Fig. 88B) **197**

– A4–13 not noticeably different from A3, without shiny scales **200**

197 Smaller, 7–8 mm. Tergal discs finely shagreened, more or less smooth and shiny, with deep and distinct punctures, punctures on disc of T1 separated

by 1–2 puncture diameters, on discs of T2–4 separated by 0.5–1 puncture diameter. Tergal margins broadly lightened yellow-orange hyaline **198**

– Larger, 10–11 mm. Tergal discs shagreened to coarsely microreticulate, at most weakly shiny, with fine regular punctures or coarse 'crater punctures'. Tergal margins at most with their apical rims narrowly lightened hyaline brown **199**

198 Clypeus, scutum, and scutellum laterally shagreened, medially smooth and shiny (Fig. 88B). Restricted to temperate areas in northern Portugal and Spain ....***fulvago* (Christ)**

– Clypeus, scutum, and scutellum microreticulate and dull. Widespread across Iberia ....***hesperia* Smith**

199 Terga shagreened, weakly shiny, with fine and dense punctation. Tergal margins comparatively weakly depressed, with narrow tight apical white hair bands. Hind basitarsi dark. Throughout Iberia.. ....***hypopolia* Schmiedeknecht**

– Terga strongly microreticulate, with coarse 'crater punctures'. Tergal margins comparatively strongly depressed, with long loose white apical hair bands that exceed the length of the marginal areas. Hind basitarsi lightened orange. Restricted to high altitude sites (>1200 m) in the Pyrenees............ ....***ranunculorum* Morawitz**

200 Larger species, 12–14 mm, usually with abundant black, white, or brown pubescence, usually with entirely dark black facial hair. Ocelloccipital distance >2 times the diameter of a lateral ocellus. Terga always without apical hair bands, sometimes with lateral hair patches (*Melandrena* partim)....201

– Smaller species, 9–10 mm, usually with subdued pubescence, facial hairs often pale, though dark in *A. lepida* and *A. propinqua*. Ocelloccipital distance often shorter, <2 times the diameter of a lateral ocellus. Terga with or without hair bands..**207**

201 Face and mesepisternum with long white pubescence, mesosoma dorsally with bright light brown pubescence. Univoltine, flying April-June. Restricted to temperate parts of northern Spain[27] ....***nitida* (Müller)**

– Without this pattern of pubescence; face either with extensive dark pubescence, or mesepisternum with dark pubescence, or mesosoma dorsally with dark pubescence..**202**

202 Body with only black and white pubescence **203**

– Body with at least some brown pubescence..**204**

27 Note, separation of *Melandrena* species in this group is usually made on the basis of colouration. However, these taxa are extremely variable, and certain characters that work in elsewhere in Europe do not work in Iberia. Caution should be taken; powerful genetic techniques are required to robustly delineate these species in an Iberian context.

203 Body typically more extensively dark haired, face and mesepisternum normally with entirely black hairs. T2–4 laterally with strongly contrasting dense patches of white pubescence[28] .... ***albopunctata* (Rossi)**

– Body often with extensive pale hairs, face sometimes white-haired with black hairs laterally, sometimes entirely black-haired. Terga often entirely black haired, laterally without dense patches of white pubescence. In pale forms, if T2–4 have loose white hair fringes laterally, then mesepisternum always white-haired[28] .... ***morio* Brullé**

204 Terga shagreened, obscurely punctate, with punctures disappearing into the underlying sculpture .... ***assimilis* Radoszkowski**

– Terga at most weakly shagreened, sometimes smooth and shiny, at least weakly shiny. Discs of T2–5 clearly and usually densely punctate, punctures typically separated by 1 puncture diameter **205**

205 Marginal areas of terga with narrow section of apical rim lightened hyaline-brown, tergal discs with weak bronzy reflections. Face with mixture of dark brown and black hairs.. ***nigroaenea* (Kirby)**

– Marginal areas of terga with apical rim dark, not lightened, tergal discs dark, without weak bronzy reflections. Face with uniformly black hairs **206**

206 Disc of T1 with dense punctures, punctures separated by up to 2 puncture diameters[29] .... ***limata* Smith**

– Disc of T1 with more scattered punctures, punctures usually separated by over 3 puncture diameters[29] .... ***thoracica* (Fabricius)**

207 A3 extremely short, at most 0.5 times the length of A4[30] **208**

– A3 longer, at least 0.8 times as long as A4, often as long as A4..............**209**

208 Facial hair almost entirely black, with a few scattered light brown hairs around the antennal insertions. Clypeus densely punctate, punctures separated by 0.5 puncture diameters, underlying surface smooth and shiny. Widespread across Iberia.. ***lepida* Schenck**

– Facial hair intermixed light and dark. Clypeus more sparsely and irregularly punctate, punctures separated by 1–2 puncture diameters, underlying surface microreticulate and dull. Very rare, known only from one specimen from Cádiz .... ***rhypara* Pérez**

209 Genital capsule distinctive, elongate, basally narrowed (Fig. 92A). Tergal discs with punctation becoming sparser laterally, most clearly visible on T2 ....**210**

– Genital capsule otherwise. Tergal discs with uniform punctation **211**

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28 These two species can be tricky to separate due to large colour variation within *A. morio* following the synonymy of the more extensively pale-haired *A. hispania*. Association with females should be made.

29 These two species are very difficult to separate in the male sex, and positive determination is not possible in many cases.

30 Note, male *Simandrena* are very difficult to identify; association should be made with females.

210 Face with predominantly dark hairs, with some light hairs intermixed around the antennal insertions. Scutum polished, shiny. Hind tarsi dark. Common throughout Iberia .... ***propinqua* Schenck**

– Face with entirely light hairs. Scutum shagreened and dull. Hind tarsi lightened orange. Restricted to temperate areas in northern Spain ....***dorsata* (Kirby)**

211 Face with entirely bright pubescence, without any dark hairs laterally. Terga entirely smooth and shiny, without shagreenation .... ***combinata* (Christ)**

– Face with at least some dark hairs laterally. Terga often with shagreenation **212**

212 Terga entirely shagreened and dull to weakly shiny at most. Clypeus with fine granular shagreen, relatively shallowly punctate, medially with weak impunctate longitudinal midline. Discs of T2–4 densely punctate, punctures separated by 0.5 puncture diameters........................... ***antigana* Pérez**

– Terga less strongly shagreened, weakly to strongly shiny. Structure of clypeus variable, from shagreened to smooth and shiny, more strongly and deeply punctate. Terga less densely punctate, punctures on discs of T2–4 separated by at least 1 puncture diameter **213**

213 Mesepisternum and propodeum with abundant black-brown hairs; remaining pubescence whitish. Scutum comparatively less strongly shagreened, weakly shiny. Restricted to areas close to the Pyrenees ....***thomsonii* Ducke**

– Mesepisternum, dorsum of mesosoma, and propodeum with bright yellowish pubescence, at most with occasional scattered black hairs. Scutum comparatively more strongly shagreened, dull...**214**

214 Clypeus between the punctures smooth and shiny. Tergal discs without shagreen, smooth and shiny, clearly visible at the base of T2. More widespread across Iberia[31] .... ***congruens* Schmiedeknecht**

– Clypeus between the punctures shagreened, at most weakly shiny. Tergal discs shagreened, weakly shiny, most clearly visible on the base of T2. Restricted to the Pyrenees and Cantabrian Mountains[31] .... ***confinis* Stöckhert**

215 (193) Genital capsule unique within the Iberian fauna (Fig. 92B). Restricted to the Pyrenees and Cantabrian Mountains ....***polita* Smith**

– Genital capsule otherwise **216**

216 Head elongate, only slightly wider than long. Clypeus shagreened and dull in its basal half, polished and shiny in its apical half (Fig. 54C). Mesepisternum laterally with long strongly plumose light brown hairs (Fig. 54A). Genital capsule simple, with penis valves progressively narrowing apically (Fig. 54F). Known only from south-western Spain (Cádiz, Sevilla), flying in the very early spring (January–March) .... ***ramosa* Wood**

– Combination of characters otherwise...**217**

31 These two species are challenging to separate, and there may be taxonomic complexity in Iberia as well as across Europe. Further study is required.

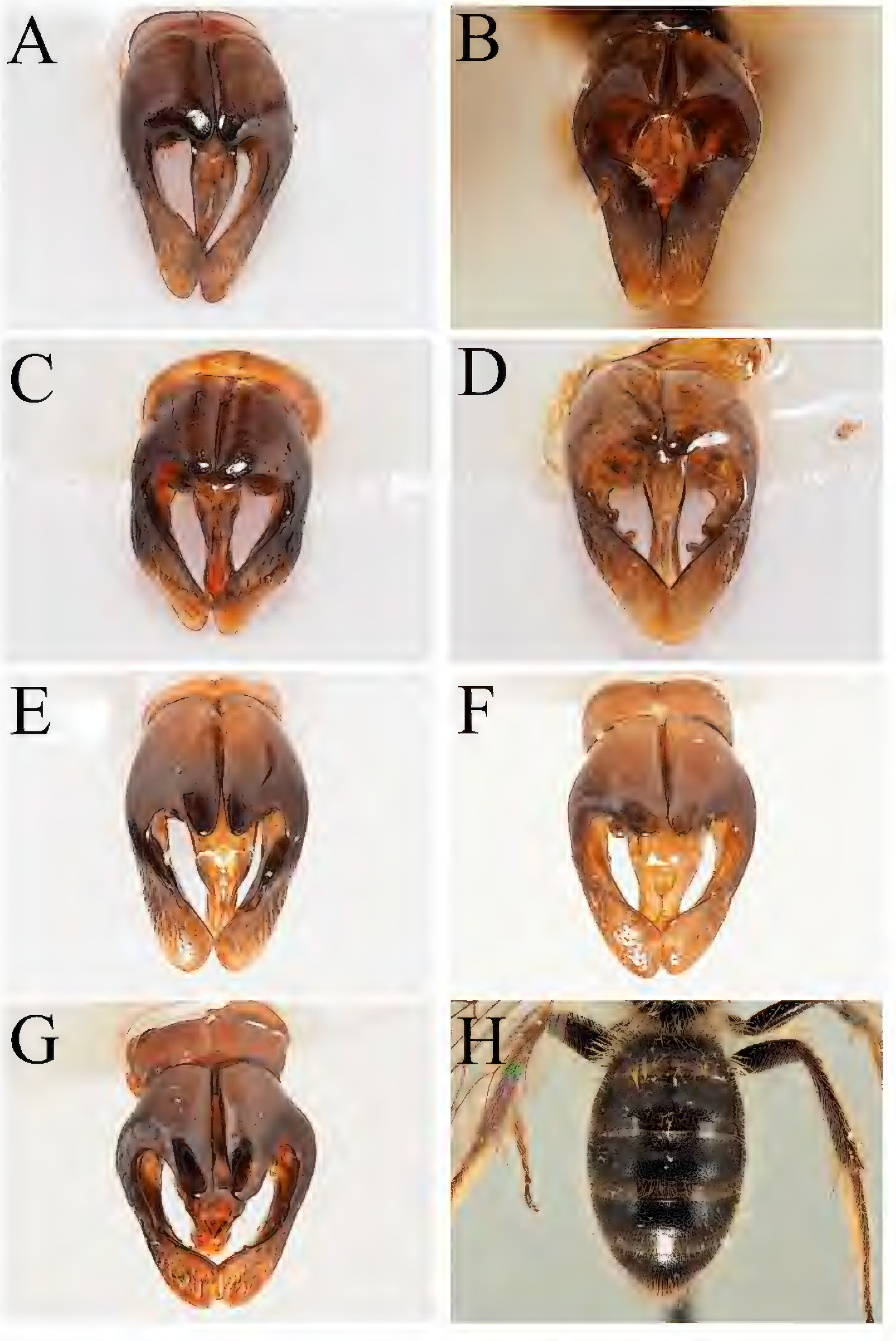

Figure 92. *Andrena* (*Simandrena*) *propinqua* Schenck, 1853, male **A** genital capsule, dorsal view; *Andrena* (*Ulandrena*) *polita* Smith, 1847, male **B** genital capsule, dorsal view; *Andrena* (*Euandrena*) *granulosa* Pérez, 1902, male **C** genital capsule, dorsal view **H** terga, dorsal view; *Andrena* (*Euandrena*) *bicolor* Fabricius, 1775, male **D** genital capsule, dorsal view; *Andrena* (incertae sedis) *corax* Warncke, 1975, male **E** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *parviceps* Kriechbaumer, 1873, male **F** genital capsule, dorsal view; *Andrena* (*Leucandrena*) *argentata* Smith, 1844, male **G** genital capsule, dorsal view.

217 Clypeus domed, covered with dense network of coarse and strongly raised transverse wrinkles. Dorsolateral surface of propodeum with dense network of raised rugosity that is almost indistinguishable from the propodeal triangle, this network extending onto the lateral faces of the propodeum. Terga smooth and shiny with regular deep punctures, without a hint of shagreenation.. ***ampla* Warncke**

– Without this combination of characters... **218**

218 Tergal margins distinctly depressed, depressions medially occupying 40% of the visible segment (Fig. 89C). Tergal discs densely punctate, punctures separated by 0.5–1 puncture diameters; tergal margins impunctate, lightened hyaline brown, strongly contrasting tergal discs. Margins of T2–4 basally with long whitish plumose hairs that arise from the junctions with the discs and overly the marginal areas without obscuring the underlying surface. Facial pubescence uniformly whitish. Terga often reddish laterally, view in profile .... ***hystrix* Schmiedeknecht** (*partim*)

– Without this combination of characters... **219**

219 Penis valves narrow, more or less parallel-sided along their length (Fig. 92C, D; *Didonia* and remaining *Euandrena*) **220**

– Penis valves basally broadened, clearly wider basally than medially or apically (Fig. 92E–G) **225**

220 Head relatively elongate. Process of the labrum large, slightly wider than long. Clypeus domed, with large irregular punctures, punctures separated by 0.5–2 puncture diameters, with unclear impunctate longitudinal midline. In fresh specimens, terga with clear unbroken apical hair fringes. Bivoltine, March-April and again in June-July......................... ***mucida* Kriechbaumer**

– Head less elongate. Process of the labrum smaller, more clearly wider than long. Clypeus more weakly domed, shiny to shagreened. Terga without apical hair fringes **221**

221 Apical margins of T1–5 widely lightened hyaline-yellow (Fig. 92H). Terga impressed basally and apically, thus tergal discs appear humped. Species associated with Cistaceae **222**

– Tergal margins at most with apical margins narrowly lightened yellowish. Tergal discs comparatively flat. Species not strongly associated with Cistaceae **223**

222 Base of terga and tergal margins comparatively strongly impressed, margins clearly separated from disc by a visible 'step' (Fig. 92H). Tergal discs coarsely and densely punctate, punctures separated by 2 puncture diameters[32]......... .... ***granulosa* Pérez**

– Base of terga and tergal margins comparatively weakly impressed, margins not clearly separated from discs by a visible 'step', almost level with discs medially. Tergal discs less densely punctate, punctures separated by 3–4 puncture diameters[32]... ***vulpecula* Kriechbaumer**

32 These two species are difficult to separate morphologically. Comparison with confidently determined reference material should be made.

223 Gonostyli apically truncate, outer margin forming an acute point. A3 only slightly longer than A4. Pubescence entirely light brown with exception of occasional dark hairs laterally on the face. Restricted to temperate areas close to the Pyrenees...***rufula*** **Schmiedeknecht**

– Gonostyli with outer margin rounded, never forming an acute point. A3 visibly longer than A4...**224**

224 Light hairs on dorsal parts of mesosoma, terga and sterna yellowish white in fresh specimens. Erect hairs on disc of T4 usually predominantly dark. Facial pubescence often entirely dark. Bivoltine, can be recorded between March and August. Widespread across Iberia[33] ...... ***bicolor*** **Fabricius sensu lato** (two mitochondrial lineages are present in *A. bicolor*; to date, only the southern lineage has been found in Iberia)

– Light hairs on dorsal parts of mesosoma, terga and sterna snow white, without yellowish hue even in very fresh specimens. Disc of T4 at most with a few isolated, erect dark hairs. Face always with some grey-white hairs medially, at least between and around antennal sockets. Univoltine, April-June. Restricted to mountainous areas in northern and north-western Spain[33]...***allosa*** **Warncke** (note, the Spanish taxon may be distinct from populations in Central Europe)

225 Face medially with white hairs, laterally with clear line of black hairs along the inner margin of the clypeus. Genital capsule with outer margins of gonostyli weakly emarginate. Rare, restricted to the Pyrenees ....***gravida*** **Imhoff** (*partim*)

– Face entirely pale-haired, at most with scattered black hairs laterally. Genital capsule with outer margins of gonostyli straight, without emargination **226**

226 Terga very weakly shagreened, more or less smooth and shiny. Tergal discs with extremely scattered punctures, punctures separated by 3–4 puncture diameters or more. Genital capsule, see Fig. 92F.. ....***parviceps*** **Kriechbaumer** (*partim*, dark form)

– Terga either more strongly microreticulate (at least on discs of T2–3) or clearly and densely punctate, punctures separated by 1–2 puncture diameters..**227**

227 Tergal discs finely microreticulate, with obscure and scattered punctures, punctures separated by 2–4 puncture diameters. Tergal margins with narrow broadly interrupted hair fringes apically.......................***barbilabris*** **(Kirby)**

– Tergal discs at most finely shagreened, more or less smooth and shiny, clearly and regularly punctate, punctures separated by 1–2 puncture diameters. Tergal margins with narrow interrupted or broad uninterrupted hair bands apically **228**

228 Tergal discs with punctures slightly sparser, separated by 2 puncture diameters. T2–4 apically with broad uninterrupted apical white hair bands, these

33 Note, the Spanish male of *A. allosa* is unknown, therefore this couplet is based on the key of Praz et al. (2019) for the Alps.

exceeding the length of the tergal margins and obscuring the underlying surface. Ocelloccipital distance equals the diameter of a lateral ocellus. Genital capsule, see Fig. 92G. Restricted to mountainous areas of central and northern Spain.................................***argentata* Smith** (*partim*, large individuals)

– Tergal discs with punctures slightly denser, separated by 1 puncture diameter. T2–4 apically with widely interrupted narrow lateral hair fringes. Ocelloccipital distance equals 2 times the diameter of a lateral ocellus. Genital capsule, see Fig. 92E. More widespread in central and southern Iberia........ ....***corax* Warncke**

Discussion

At 228 species, the Iberian fauna is slightly larger than those of Greece (c. 220) and Israel (c. 220), though the fauna of Israel is likely to eventually be larger than that of Iberia following ongoing revisions (Pisanty et al. 2022a). Within the Old World fauna, it is much smaller than that of Turkey which has an estimated 376 species (Wood 2023b), but this is less surprising as Turkey is larger (783,000 km^2 versus 583,000 km^2), sits at the interface of Europe and Asia, hosts an even greater diversity of habitats, and is likely at the centre of diversity for this genus (Pisanty et al. 2022b). Iberia nevertheless hosts one of the top five largest *Andrena* faunas globally.

There are a number of outstanding problems that remain to be resolved, in addition to those highlighted above. Members of the subgenus *Avandrena* Warncke remain difficult to interpret due to their morphological variation and rarity in collections. *Andrena* (*Avandrena*) *avara* Warncke, 1967 sensu stricto was described from Morocco and also occurs in southern Iberia. Two additional subspecies were described from Spain, *A. avara gavia* Warncke, 1974 (*locus typicus* Madrid in central Spain) and *A. avara liturata* Warncke, 1974 (*locus typicus* Sierra de Guadarrama in central Spain), as well as two additional subspecies from North Africa. These may all represent valid species; molecular revision of this subgenus across the West Palaearctic is necessary to define species boundaries, and also to establish whether members of the *Avandrena* that lack spines on the posterior face of the hind femur truly belong here (Pisanty et al. 2022b). Many other groups have subspecies which Warncke described from Iberia, most pertinently *A.* (*Micrandrena*) *pandosa trigona* Warncke, 1975, *A.* (*Notandrena*) *langadensis albipila* Warncke, 1967, and *A.* (*Truncandrena*) *medeninensis donata* Warncke, 1967. These may also represent valid species, but without genetic data it is unwise to raise them to species status, as the results presented here illustrate that the relationships between Iberia, North Africa, and the rest of continental Europe are not always straightforward.

A total of 33 of the 228 *Andrena* species recorded here are endemic to the peninsula (14.5%). Twenty-two of the species are true Spanish endemics (9.6% endemic), whereas no species are endemic to Portugal. Of these 33 species, 31 of them were described after 1967 in just a handful of publications by a very limited number of

authors (Warncke 1967, 1975a; Wood et al. 2020a, 2021, 2022a; Wood and Ortiz-Sánchez 2022; Wood 2022; the current work). Only the endemic *A. pruinosa* and *A. cyanomicans* (see Kratochwil 2021) were described earlier (Erichson 1835; Pérez 1895). The fact that so many of Iberia's endemic species have only been described recently makes it difficult to conclude on a likely final pattern of richness. As our ability to distinguish between cryptic taxa has increased, so has our ability to quickly travel to areas with unusual climates, botanical communities, or biogeographical histories. A defining characteristic of bees of the genus *Andrena* is their ability to very rapidly adapt their behaviours to local conditions over evolutionary time, be that in the use of a novel or locally abundant host plant, changing their emergence date or voltinism, or surviving in drier, wetter, hotter, or colder environments. This ability likely underpins their extremely high speciation rate (Bossert et al. 2022; McLaughlin et al. 2022). For example, species described from Iberia in just the last few years include those restricted to saline soils (*Andrena juliana*), a species which uses generic Brassicaceae species but which flies at the unusual time of December (*Andrena gades*), an early emerging taxon restricted to south-western Spain which has avoided capture until very recently due to its flight period of January–March (*Andrena ramosa*), a specialist of late-flowering Apiaceae which flies during September–October (*Andrena foeniculae*), and specialists of little-used botanical families such as Crassulaceae and Geraniaceae (*Andrena omnilaevis* and *Andrena erodiorum*). Altogether, this means that until all unusual habitats and mountainous areas have been thoroughly searched across the entirety of the bee season, new species are almost guaranteed to continue to be found.

It is possible however to comment more broadly on the biogeography of Iberian bees and notable distributional patterns. Warncke (1975a) identified four major biogeographic zones on the peninsula (excluding the Balearic Islands); a) north-western and northern Iberia from Coimbra to the Pyrenees, this area hosting Central European species, b) the northern *meseta* (*Meseta Norte*), or "Old Castille" (formerly known as Castilla la Vieja), the area of elevated open habitats north of the Sistema Central to the Cantabrian range, c) the southern *meseta* (*Meseta Sur*), or "New Castille" (formerly known as Castilla la Nueva) to the Ebro Valley, the lower area of open habitats south-east of the Sistema Central to the Ebro Valley, separated by the Sistema Ibérico, and d) the coastal zone from Coimbra in the west to Cádiz in the south up to Barcelona in the north-east, this area possessing a subtropical climate with hot summers and hosting Mediterranean taxa. These categorisations are broadly correct but do not fully capture the diversity of Iberian habitats and some of the patterns of endemism and micro-endemism. As a corollary, Warncke (1975a) writes that in the driest and warmest parts of Iberia some species have evolved into their own subspecies. It is worthwhile to highlight these areas in light of taxonomic developments in the intervening years.

The most substantial change since Warncke's (1975a, 1976) Iberian revision is the study of mountain refugia and their associated fauna. The Serranía de Ronda/Sierra de las Nieves and Sierra Nevada all host endemic *Andrena* species that have diverged from Iberian or from European/North African species (*A. contracta*, *A. ghisbaini*, *A. isolata*, and *A. ortizi*). The Sistema Central to the mountains in north-western Iberia (Serra do

Gerês, Cantabrian Mountains, etc) host endemic species that prefer cooler temperatures and are associated with herbaceous plants on acidic soil (*A. benoisti*, *A. gredana*, *A. omnilaevis*). In eastern Spain, the mountain ranges of the Sistema Ibérico, Sierra de Cazorla, and smaller ranges are understudied and support distinct species (*A. levante*) and subspecies whose status should be further investigated (*A. hattorfiana nigricauda* Wood, 2021). Because the eastern mountain ranges of Spain are somewhat isolated latitudinally, with intervening low elevation areas, it is likely that many of the species present here at elevation have experienced interrupted gene flow in their recent evolutionary history (e.g. subgenus *Taeniandrena*, Wood et al. 2021; Praz et al. 2022). The links between these montane populations should be investigated to establish their status. Members of the *A. intermedia* Thomson, 1870 aggregate may well be distinct, and populations present on the Sierra Nevada -> Sierra de Cazorla -> Sistema Ibérico -> Pyrenees may each represent a different species. Whether this pattern hold true for other groups requires further study.

The elevated plateau of central Spain clearly hosts relictual *Andrena* faunal elements. This is most clearly seen for two subgenera, *Nobandrena* Warncke, 1968 and *Parandrenella* Popov, 1958. *Nobandrena* consists of 10 species from Central Europe to Central Asia (western limit Switzerland), with one species endemic to central Spain (*A. funerea* Warncke, 1975), predominantly in the provinces of Ávila, Madrid, Salamanca, and Segovia. Likewise, *Parandrenella* consists of nine species from eastern Central Europe to Central Asia and Pakistan (European western limit is Slovenia, with an additional species in north-western Africa from Morocco to Tunisia; see Scheuchl et al. 2011, also Wood et al. 2020b), with one species endemic to central Spain (*A. taxana* Warncke, 1975), known only from the provinces of Cuenca, Madrid, and Soria. *Andrena funerea* and *A. taxana* therefore represent what must have been a broader distribution for these subgenera prior to the Quaternary period, both subgenera having estimated crown ages of around 10 million years (Pisanty et al. 2022b).

More broadly, Iberia hosts several predominantly eastern species in steppic or dry areas, such as *A. lateralis* (Spain and Portugal, southern Balkans to the Central Asia), *A.* (*Melandrena*) *soror* Dours, 1872 (Spain, Morocco, Turkey), and *A. urdula* (Spain, Morocco, and Greece). Iberia has strong faunal links to Morocco, and particularly the Middle Atlas. Due to the nature of European mountain chains, outside of Iberia, raised steppic areas are rare or cover only very small areas. In Central Spain, Morocco, and Turkey, extensive raised areas (the *mesetas* of Old and New Castille) of steppic habitat can be found. This elevated steppe differs from the Great Eurasian Steppe that runs from the Pannonian basin (predominantly eastern Austria, Hungary, southern Slovakia, western Romania, northern Serbia) to Mongolia and northern China, and hosts a fauna that supports the same evolutionary lineages (e.g. *Nobandrena* and *Parandrenella*), but often contains different species, many of which are endemic. This link between Iberia and Morocco can be seen particularly strongly in the Middle Atlas. In addition to the finding of *A. relata* in the Middle Atlas (Wood et al. 2020b), another species previously considered to be endemic to Spain, *A. nebularia*, can be found on the high steppe in the eastern Middle Atlas. This link to the Middle Atlas

can also be seen on the Sierra Nevada for *A. isolata* and *A. ortizi* which are genetically most closely related to what are undescribed species in the Middle Atlas. Additional genetic work and further surveys in the Middle Atlas are likely to strengthen these links further, as well as further surveys on the Sierra Nevada and the mountains of southern Spain.

The extraordinary nature of central Spain and its rich *Andrena* fauna is well-illustrated by both historical (particularly those of Dusmet that were revised by Warncke 1975a, 1976) and recent collections. During a single eight-day period from the 13th to 19th of May 2021 in the provinces of Ávila, Guadalajara, Madrid, Segovia, and Toledo I collected a total of 70 *Andrena* species, including the Iberian endemic *A. baetica*, *A. benoisti*, *A. corax*, *A. elata*, *A. funerea*, *A. lecana*, *A. murana*, *A. parata*, *A. pruinosa*, and *A. varuga* and also the restricted *A. lateralis*, *A. monilia*, *A. nebularia*, *A. soror*, *A. relata*, and *A. urdula*. Whilst large parts of the Sistema Central mountain range are protected as nature reserves or regional parks, the same is not true for the steppe habitats at lower altitudes, both north and south of this mountain range. Most collecting sites were habitat fragments sandwiched between urban development or intensive agriculture, though some formed a mosaic with land under a lower-intensity management regime. The areas south of Madrid that were so extensively collected by Dusmet and which represent the *loci typici* for many of the species described by Warncke have either been lost to urban development or are threatened by its encroachment (e.g. *Andrena montarca* was described from Montarco which is now a suburban park). Given the endemic nature of this fauna, these areas are deserving of a greater level of protection than they currently receive.

Away from central Spain, there are more obvious links between southern Spain and the North African *Andrena* fauna. Warncke (1976) recorded three predominantly North African taxa in the extreme south of Spain, specifically *A.* (*Notandrena*) *microthorax* Pérez, 1895 (Cádiz), *A.* (*Truncandrena*) *minapalumboi* Gribodo, 1894 (Cádiz, Alicante), and *A. rhypara* (Cádiz). I have seen no other material of these species, and their current status in Spain is unclear; they may be locally extinct. In contrast, recent workers have discovered three North African species in southern Spain, namely *A.* (*Truncandrena*) *varia* Pérez, 1895 (Córdoba; Ortiz-Sánchez 2020), *A. laurivora* (Huelva and Sevilla; Wood et al. 2021), and *A. melacana* (Albacete, Cádiz, Granada, Málaga; Wood and Ortiz-Sánchez 2022). Given the lack of historical and contemporary collecting in southern Spain, it is very difficult to answer whether or not these species were always present, whether the newly detected species are recent arrivals, or whether there is a constant turnover of North African species in southern Spain that regularly colonise and then become locally extinct. Increased recording of *Andrena* specifically and Iberian bee species more broadly is required in order to better understand faunal interchanges across the Strait of Gibraltar.

Finally, the difference between the size of the Portuguese (128) and Spanish (228) *Andrena* faunas is large and notable. Though Portugal has a higher density of *Andrena* species due to its much smaller size, it hosts no endemic *Andrena* species compared to the 22 species endemic to mainland Spain. As highlighted above, the Portuguese

Andrena fauna is so much smaller due to the almost complete absence of high northern mountains and their associated Euro-Siberian fauna (the Serra da Estrella reaches to 1,993 m but is isolated from the high Cantabrian Mountains of northern Spain), the lack of elevated steppe (limited to north-eastern Portugal around Almeida or the Douro valley), the lack of high mountains in the south (the Sierra de las Nieves reaches 1,919 m and the Sierra Nevada 3,479 m), and finally the absence of the very hot and dry Mediterranean habitat from Cádiz to Alicante and Valencia that hosts both North African species as well as restricted endemic species. When taken collectively, it is this enormous variety of habitats, isolated mountains, and Atlantic and Mediterranean influences that has shaped and generated the rich Iberian *Andrena* fauna, and continues to provide taxonomic surprises and ecological delights.

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Supplementary material 1

Iberian *Andrena* species checklist

Authors: Thomas J. Wood

Data type: National checklist

Explanation note: Iberian *Andrena* species checklist, with national totals for Portugal and Spain, details on *loci typici* for species described from Iberia, and dietary niche classifications.

Link: https://doi.org/10.3897/jhr.96.101873.suppl1